Late Cretaceous *and* Cenozoic History *of* Latin American Vegetation *and* Terrestrial Environments

Alan Graham

Missouri Botanical Garden

Dear friends

You are in your house. Welcome. This misters say. You pass this night here. because the guía can not come because the way are bigger. In this city there is a hotel, is not very good, but you can pass very good night. One of this misters say that tomorrow will put men works that will can help you.

I am sorry this mite.

Your friend. Teacher. M.a del Carmen.

ISBN: 978-1-930723-68-9
Library of Congress Control Number: 2009935194

Monographs in Systematic Botany from the Missouri Botanical Garden, Volume 113
ISSN 0161-1542

Scientific Editor and Head: Victoria C. Hollowell
Managing Editor: Beth Parada
Associate Editor: Allison Brock
Editorial Assistant: Tammy M. Charron
Press Coordinator: Cirri R. Moran

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P.O. Box 299
St. Louis, Missouri 63166-0299, U.S.A.
www.mbgpress.org

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Frontispiece: Back on the road through the help of friends, between Atotonilco and Metquititlá, Mexico, in August 1965. The letter was written by the local schoolteacher, who made arrangements for work and accommodations, and it is symbolic of encounters during the decades of the author's field research in Latin America (see Preface). Photograph by the author.

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PREFACE

This book traces lineages, assemblages, and events in the history of Latin American vegetation and terrestrial paleoenvironments from just prior to the asteroid impact at the end of the Cretaceous through the turbulent times of the Holocene. It is a continuation of *Late Cretaceous and Cenozoic History of North American Vegetation (north of Mexico)* (Graham, 1999a), which includes discussions of Cause and Effect (Climate, Plate Tectonics, Catastrophes); Context (Global Marine Paleotemperature Curve, Sea-Level Curve); and Methods, Principles, Strengths, and Limitations. Some information on climate is reviewed here, but chapters 2, 3, and 4 of the introductory volume should be consulted as needed for background to the present text. To minimize repetitious citation, it is referenced here as I: (page number, chapter, or figure) where topics relevant to this volume are discussed.

BEGINNINGS AND ACKNOWLEDGMENTS

My studies in Neotropical vegetation history began in 1963 when Elso Barghoorn of Harvard University called my dissertation adviser Chester Arnold at the University of Michigan to ask if any students there were familiar with Miocene palynofloras and interested in working on an assemblage of that age from Panama. I had just completed a study of the Miocene Succor Creek and Trout Creek floras of Oregon, and Professor Barghoorn had recently obtained samples from the Panama Canal Company, used by Alexandra Bartlett for her doctoral research on Quaternary climates and sea-level changes in Panama (Bartlett & Barghoorn, 1973). These samples extended into the underlying Miocene Gatún Formation.

Preface Figure 1. Frank Hankins (left) and Elso Barghoorn examining a piece of petrified wood for which the area around David, Panama, is famous. Hankins was an avid collector of petrified wood and his extensive collections are now at Harvard University.

I began my work at Harvard University in 1963 under a postdoctoral fellowship generously supported through the Gray Herbarium and its director, Reed C. Rollins. The first field trip of the project was during Christmas of 1963–64 to collect fossil wood for the Hankins Collection (Preface Figs. 1, 2, 3) and Tertiary sediments of several ages from cores of the Panama Canal Company. The Chief Geologists of the company, Robert Stewart and later his wife, Jay Stewart, contributed much helpful information throughout the Panama studies. Samples were collected from the Gatuncillo (late Eocene), Culebra, Cucaracha, La Boca (early Miocene), and Gatún (late Miocene) formations.

The Christmas season was often unsettled in Panama, with demonstrations orchestrated to coincide with negotiations for a new lease agreement for the Panama Canal. Those in 1963 were worse than usual (Preface Fig. 4), and the months following were not a prudent time for fieldwork in Panama. Also, study of the fossil material was proving difficult because of the relatively small reference collection of about 5000 slides and the few general summaries available on the modern communities, their composition, distribution, and ecology. Meanwhile, samples had been obtained from the middle Oligocene San Sebastián Formation of Puerto Rico through the cooperation of Reginald Briggs and Othmar Tobisch (U.S. Geological Survey, San Juan). The extant vegetation of the Antilles was comparatively well known from the work of Richard Howard and others. The National Science Foundation began supporting my studies on the Tertiary vegetation and paleoenvironments of Latin America in 1967 under the project, "Studies in Neotropical Paleobotany," and the San Sebastián fossil flora was the first published in that series (Graham & Jarzen, 1969). The second was on the middle Pliocene Paraje Solo flora near Coatzacoalcos, Veracruz, Mexico (Graham, 1976). The Mexican project was facilitated through introductions by Arturo Gómez-Pompa (UC MEXUS, Riverside, California) to Agustín Ayala-Castañares (UNAM) and Guillermo P. Salas (UNAM, PEMEX), who provided locality data and access to PEMEX sites in southeastern Mexico. Field associates in Mexico were students Enrique Martínez-Hernández (now at the Instituto Geología, UNAM) and David Jarzen (Florida Museum of Natural History). Arturo Gómez-Pompa accompanied me on a field trip to Veracruz that included study of the cloud forest, which proved valuable in interpreting the Paraje Solo vegetation.

The third project, initiated in 1980, was to be on Neogene palynofloras from Guatemala. Political unrest made it impossible to do the fieldwork, but in the meantime things had settled down in Panama. Also, the *Flora of Panama* (Woodson

et al., 1943 et seq.; D'Arcy, 1987a, b; D'Arcy & Correa A., 1985) was nearing completion, the *Flora of Barro Colorado Island* (Croat, 1978) was available, and it was possible to conclude the Panama project in 1991 (Graham, 1985, 1988a, b, 1989, 1991a, b, c; Graham et al., 1985). The Guatemala study was completed 18 years after it was initiated (Graham, 1998), through the cooperation of Gabriel Dengo (Centro Estudios Geológicos América Central, Guatemala City) and Burke Burkart (University of Texas, Arlington).

Data on the vegetation history of Costa Rica came from the middle Pliocene Uscari sequence (Graham, 1987) and from the Pliocene Río Banano Formation (Graham & Dilcher, 1998). Luis D. Gómez arranged a field trip to the Cerro de la Muerte in the Cordillera Talamanca that provided helpful insights into the modern vegetation of Costa Rica. Another plant microfossil flora was recovered from the Oligo–Miocene La Quinta Formation of Chiapas, Mexico (Graham, 1999b), and studied in cooperation with Rodolfo Palacios Chávez (Instituto Politecnico National, Mexico City; Graham & Palacios Chávez, 1996). Throughout the studies in Mexico, Jerzy Rzedowski provided information on the modern vegetation and other courtesies that are sincerely appreciated.

Fossil palynofloras from the Antilles include the Mio–Pliocene Artibonite flora from Haiti (Graham, 1990), with grateful acknowledgment to Walter Judd (University of Florida, Gainesville) and Dan Skean (Albion College, Albion, Michigan); the middle Eocene Guys Hill Formation of Jamaica (Graham, 1993), with the collaboration of Edward Robinson and Stephen Donovan (University of the West Indies, Kingston, Jamaica); and the middle Eocene Saramaguacán flora of Cuba (Graham et al., 2000), co-authored with student Duane Cozadd, Alberto Areces-Mallea (San Juan, Puerto Rico), and Norman Frederiksen (U.S. Geological Survey, Reston, Virginia). These studies have also benefited from discussions on Antillean geology with Paul Mann (Institute for Geophysics, University of Texas, Austin), James Pindell (Tectonic Analysis, Ltd., West Burton, U.K.), and Manuel Iturralde-Vinent (Museo Nacional de Historia Natural, Havana, Cuba).

The South American studies began with an invitation from Omar Colmenares (Centro Investigación Desarrolo Filial Petróleos Venezuela, INTEVEP) to consult on an Eocene section from the Maracaibo Basin. Another study was on a Mio–Pliocene flora from the Eastern Cordillera of the Bolivian Andes (Graham et al., 2001), supported by the National Geographic Society and co-authored with Kathryn Gregory-Wodzicki (Lamont-Doherty Earth Observatory) and student Kari Wright. Michael Nee (NY) accompanied me on a field trip to the cloud forests of Bolivia, and further information on the modern vegetation was provided by Peter Jørgensen and James Solomon (MO).

Other individuals have given valuable assistance in a variety of ways throughout the study. In particular, access to spore and pollen herbarium material was made possible through David Lellinger, Joan Nowicke, and Stanwyn Shetler (US); Patricia Holmgren (NY); and Nancy Morin (MO). This access was essential in building the reference collection to its present size of about 25,000 slides. Through the good offices of Director Peter Raven, I was a research associate at the Missouri Botanical Garden (MO) between 1975 and 2003, and curator of paleobotany and palynology since that time, with access to the expertise of the research staff and the extensive library, databases, and herbarium collections. The year 1969–70 was spent at the University of Amsterdam working on the Panama material, and that visit included many valuable discussions on the paleoecology of northern South America with Thomas van der Hammen and T. J. Wijmstra. Another visit was made to Panama in 1990 to the Smithsonian Tropical Research Institute (STRI) as part of its Senior Visiting Scholars Program through the courtesy of David Roubik.

Preface Figure 2. The Posada San Sebastián at David, Panama. The entire façade of the posada is made of petrified wood. The age of the wood is unknown, but it is likely Neogene, possibly Miocene.

Shirley A. Graham has taken many of the photographs, reviewed most of the manuscripts, and has been a field associate throughout the project, in addition to pursuing her own research on the taxonomy of the Lythraceae. Her efforts are sincerely appreciated and deserve special acknowledgment.

Others providing field and technical assistance, information, photographs, literature, reviews, and/or permission to use published and unpublished material are Sandra Arango-Caro, Paul Baker, Viviana Barreda, Mike Blomberg, William Buck, Robyn Burnham, Mark Bush, Taciana Cavalcanti, Paul Colinvaux, Laurel Collins, Trisha Consiglio, Mireya Correa, Georgina Del Fueyo, Thomas Donnelly, Grenville Draper, Ismael Ferrusquía-Villafranca, Julio Figueroa, Michael Grayum, Barry Hammel, Henry Hooghiemstra, Sally Horn, Trevor Jackson, Carlos Jaramillo, Iván Jiménez, David Lea, Barbara Leyden, Lúcia Lohmann, María Socorro Lozano-García, Michael Macphail, Steven Manchester, Enrique Martínez-Hernández, Sarah Metcalfe, Barbara Mohr, Olga Martha Montiel, Scott Mori, Kevin Nixon, Anthony Orme, E. G. Ottone, Dolores Piperno, Jay Quade, Susanne Renner, Andrea Schwarzbach, Alan Smith, Mario Sousa S., W. Douglas Stevens, Donald Stone, Charlotte Taylor, Alice Tryon, Rolla Tryon, Carmen Ulloa Ulloa, Thomas Van Devender, Bruno M. T. Walter,

Preface Figure 3. Courtyard of the Posada San Sebastián. The eggs were placed among the plants prior to our arrival to deflect glances of those suspected of having "the evil eye."

Reinhard Weber, Tom Wendt, and the many other persons acknowledged with gratitude in the primary publications. Opportunity for exchange of information on the biology and geology of the Antilles was made possible through the NESCent Conference, Biological Diversification on the West Indian Archipelago (Punta Cana, Domican Republic, 5–9 July 2006). The book benefited considerably from the editorial talents of Eileen P. Duggan, Allison Brock, Beth Parada, and Victoria C. Hollowell, scientific editor of the Missouri Botanical Garden Press. Sources of photographs and copyright holders granting permission to use illustrations are listed in the legends. In a very few instances, it has proven impossible to reach a publisher, author, and/or estate for permission after best-intent efforts. These are indicated in the legends with the source of the illustration and the author provided. All uncredited photographs and illustrations are by the author.

The publications cited above are only a small part of the extensive literature on Latin American vegetation and vegetation history contributed over a span of 150 years by both foreign and resident scientists. The perseverance and dedication of the early workers in the American tropics warrant special admiration and respect—e.g., Arana, Bates (Clodd, 1892); Cabral, de Aguirre, de Orellana, de Teixeira, the Godins, Wickman, and others (Smith, 1990); Darwin, La Condamine, Spruce, von Humboldt (von Hagen, 1945; Seaward & Fitzgerald, 1996); Palmer (McVaugh, 1956); Pringle (Davis, 1936); Wallace (Knapp, 1999; Raby, 2001; Berry, 2002; Camerini, 2002; Shermer, 2002); Ruiz and Pavón (Steele, 1964), and others. Excerpts from the writings of these early authors are reprinted in Chazdon and Whitmore (2002). The fieldwork of numerous early geologists and paleobotanists such as V. Auer, E. W. Berry, E. Dolianiti, J. Felix, J. Frenguelli, A. Hollick, E. P. Oliveira, F. W. Sommer, and others was equally arduous, and their contributions are acknowledged at appropriate places in the text.

All who have been privileged to work in Latin America are aware of the legendary courtesies of colleagues, and the inevitable experiences that can alleviate the difficulties and frustrations of fieldwork. Two examples are given here to illustrate why so many people initially drawn to Latin America choose to spend their careers studying the natural history of the region. In August 1965, we were searching for a locality along the path between Atotonilco and Metquititlán, Hidalgo, Mexico. Our truck slipped off the road into a deep hole in front of a culvert that funneled water from the nearby mountains into a canyon below. It started to rain, giving every indication that the truck would be swept into the canyon. It was getting dark, and a man offered to walk with us into the nearest village about 5 km away, where the local teacher of English made arrangements for accommodations and for help in digging the truck out the following morning. It rained off and on throughout the night, and although not heavy, it resounded ominously on the tin roof and gave visions of National Science Foundation's truck careening down the canyon in a torrent of water. We got the truck out, and the letter written by the teacher, María del Carmen, remains a valued reminder of the experience (frontispiece).

An episode that provided some much-needed levity occurred in 1962 while we were camping in a trailer park in Guadalajara, Mexico. We were tenting and during rainy nights slept in the car. The accommodations were beginning to lose their magic, when there pulled into the park a vehicle that made ours seem luxurious. It was a large yellow school bus that had a hole cut in the roof, and mounted on top was the body of a Nash Rambler serving as an observation deck. It looked like a bizarre accident, but the American family of five seemed to enjoy the attention and were having a grand time.

The information presented in this text represents a synthesis of nearly 50 years of study and fascination with the history, culture, and vegetation of Latin America. My deep appreciation goes to the supporting foundations, institutions, corporations, and the many colleagues who have made it possible.

REFERENCES

Bartlett, A. S. and E. S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (A history of vegetation, climate, and sea-level change). *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 203–299.

Berry, A. (ed.). 2002. Infinite Tropics: An Alfred Russel Wallace Anthology. Verso, London.

Camerini, J. R. (ed.). 2002. The Alfred Russel Wallace Reader: A Selection of Writings from the Field. The Johns Hopkins University Press, Baltimore.

Chazdon, R. L. and T. C. Whitmore. 2002. Foundations of Tropical Forest Biology. University of Chicago Press, Chicago.

Clodd, E. 1892. Bates' River Amazons: The Naturalist on the River Amazons. John Murray, London.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, CA.

D'Arcy, W. G. 1987a. Flora of Panama, Checklist and Index. Part I. The Introduction and Checklist. Monogr. Syst. Bot. Missouri Bot. Gard. 17.

———. 1987b. Flora of Panama, Checklist and Index. Part II. Index. Monogr. Syst. Bot. Missouri Bot. Gard. 18.

——— and M. D. Correa A. 1985. The Botany and Natural History of Panama: La Botánica e Historia Natural de Panamá. Missouri Botanical Garden, St. Louis.

Davis, H. B. 1936. Life and Work of Cyrus Guernsey Pringle. University of Vermont, Burlington.

Graham, A. 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63: 787–842.

———. 1985. Studies in neotropical paleobotany. IV. The Eocene communities of Panama. Ann. Missouri Bot. Gard. 72: 504–534.

———. 1987. Miocene communities and paleoenvironments of southern Costa Rica. Amer. J. Bot. 74: 1501–1518.

———. 1988a. Studies in neotropical paleobotany. V. The lower Miocene communities of Panama—the Culebra Formation. Ann. Missouri Bot. Gard. 75: 1440–1466.

———. 1988b. Studies in neotropical paleobotany. VI. The lower Miocene communities of Panama—the Cucaracha Formation. Ann. Missouri Bot. Gard. 75: 1467–1479.

———. 1989. Studies in neotropical paleobotany. VII. The lower Miocene communities of Panama—the La Boca Formation. Ann. Missouri Bot. Gard. 76: 50–66.

———. 1990. Late Tertiary microfossil flora from the Republic of Haiti. Amer. J. Bot. 77: 911–926.

———. 1991a. Studies in neotropical paleobotany. VIII. The Pliocene communities of Panama—introduction and ferns, gymnosperms, angiosperms (monocots). Ann. Missouri Bot. Gard. 78: 190–200.

———. 1991b. Studies in neotropical paleobotany. IX. The Pliocene communities of Panama—angiosperms (dicots). Ann. Missouri Bot. Gard. 78: 201–223.

———. 1991c. Studies in neotropical paleobotany. X. The Pliocene communities of Panama—composition, numerical representations, and paleocommunity-paleoenvironmental reconstructions. Ann. Missouri Bot. Gard. 78: 465–475.

———. 1993. Contribution toward a Tertiary palynostratigraphy for Jamaica: The status of Tertiary paleobotanical studies in northern Latin America and preliminary analysis of the Guys Hill Member (Chapelton Formation, middle Eocene) of Jamaica. *In:* R. M. Wright and E. Robinson (eds.), Biostratigraphy of Jamaica. Geol. Soc. Amer. Mem. 182: 443–461.

———. 1998. Studies in neotropical paleobotany. XI. Late Tertiary vegetation and environments of southeastern Guatemala: Palynofloras from the Mio–Pliocene Padre Miguel Group and the Pliocene Herrería Formation. Amer. J. Bot. 85: 1409–1425.

———. 1999a. Late Cretaceous and Cenozoic History of North American Vegetation (north of Mexico). Oxford University Press, Oxford, U.K.

Preface Figure 4. Rioted Pan American Building, Panama City, Panama, seen from the grounds of the former Tivoli Hotel, Canal region, December 1963.

———. 1999b. Studies in neotropical paleobotany. XIII. An Oligo–Miocene palynoflora from Simojovel (Chiapas, Mexico). Amer. J. Bot. 86: 17–31.

———, D. Cozadd, A. Areces-Mallea, and N. O. Frederiksen. 2000. Studies in neotropical paleobotany. XIV. A palynoflora from the middle Eocene Saramaguacán Formation of Cuba. Amer. J. Bot. 87: 1526–1539.

——— and D. L. Dilcher. 1998. Studies in neotropical paleobotany. XII. A palynoflora from the Pliocene Río Banano Formation of Costa Rica and the Neogene vegetation of Mesoamerica. Amer. J. Bot. 85: 1426–1438.

———, K. M. Gregory-Wodzicki, and K. L. Wright. 2001. Studies in neotropical paleobotany. XV. A Mio–Pliocene palynoflora from the Eastern Cordillera, Bolivia: Implications for the uplift history of the Central Andes. Amer. J. Bot. 88: 1545–1557.

——— and D. M. Jarzen. 1969. Studies in neotropical paleobotany. I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308–357.

——— and R. Palacios Chávez. 1996. Additions and preliminary study of an Oligo–Miocene palynoflora from Chiapas, Mexico. Rheedea 6: 1–12.

———, R. H. Stewart, and J. L. Stewart. 1985. Studies in neotropical paleobotany. III. The Tertiary communities of Panama—geology of the pollen-bearing sediments. Ann. Missouri Bot. Gard. 72: 485–503.

Knapp, S. 1999. Footsteps in the Forest: Alfred Russel Wallace in the Amazon. The Natural History Museum, London.

McVaugh, R. 1956. Edward Palmer: Plant Explorer of the American West. University of Oklahoma Press, Norman.

Raby, P. 2001. Alfred Russel Wallace: A Life. Princeton University Press, Princeton, NJ.

Seaward, M. R. D. and S. M. D. Fitzgerald (eds.). 1996. Richard Spruce (1817–1893): Botanist and Explorer. Royal Botanic Gardens, Kew, Richmond, U.K.

Shermer, M. 2002. In Darwin's Shadow: The Life and Science

of Alfred Russel Wallace. A Biographical Study on the Psychology of History. Oxford University Press, Oxford, U.K.

Smith, A. 1990. Explorers of the Amazon. University of Chicago Press, Chicago.

Steele, A. R. 1964. Flowers for the King: The Expedition of Ruiz and Pavón and the Flora of Peru. Duke University Press, Durham, NC.

von Hagen, V. W. 1945. South America Called Them: Explorations of the Great Naturalists La Condamine, Humboldt, Darwin, Spruce. Alfred A. Knopf, New York.

Woodson, R. E., Jr., R. W. Schery, and collaborators. 1943 et seq. Flora of Panama. Ann. Missouri Bot. Gard., vol. 30 et seq.

PROLOGUE

The tropical regions of the Earth contain the greatest concentration of organisms and communities of organisms on the planet. Understanding their origin, diversification, migration, current status, and value in the broadest sense and developing workable policies of conservation and sustainable development constitute some of the most challenging problems ever to face humankind (Achard et al., 2002; Balmford et al., 2002; Leshner, 2002; Mann, 2002; Raven, 2002). Fortunately, this is a time when a vast array of methodologies are available for investigating tropical biotas and the environments in which they evolved. It is almost routine to accept that we can now determine the CO_2 concentration of the Earth's atmosphere over the past 100 million years; reconstruct temperatures through eons of geologic time as changes in the Earth's position relative to the sun determine the amount, and alterations in ocean and atmospheric currents determine the distribution, of heat and cold; detect fluctuations in ancient ozone levels from the amounts of DNA-protecting pigments in *Lycopodium* spores (Lomax cited in Morton, 2005); trace patterns of precipitation from mite floras preserved in stalagmites; estimate how high mountains were at different stages in their history; follow cycles of drought from the titanium content of basin sediments; relate these cycles to the rise and fall of the great ceremonial centers of Latin America; determine how long El Niños and La Niñas have perturbated global climates; assign absolute ages to these events based on ^{10}Be and other isotopes; and compare the appearance of lineages in the fossil record with divergence times and evolutionary patterns based on combined morphological and multiple-gene phylogenies. These are remarkable achievements, and it is an exciting time to be investigating patterns, processes, cycles, and events of global and extraterrestrial origin that have interacted with the biota to produce some of the Earth's most complicated ecosystems.

The telling of this history presents formidable problems of synthesis and organization, and many different paths could be followed. The one taken here traces the history of Latin American vegetation and terrestrial paleoenvironments from the Late Cretaceous through the Cenozoic, identifies the concatenation of causal factors involved in the modernization of the vegetation, appraises the reconstructed history in the context of results from independent lines of inquiry, describes methods, emphasizes the broader value or "so-whatness" of the information, and provides a guide to the literature to facilitate further study and encourage independent assessments. The traditional approaches are either stratigraphic (viz., by time intervals) or geographic (by country or region). The principal disadvantage to both is that they compartmentalize the subject into discrete segments. This complicates treating events that involve more than one region and processes that extend over time, such as the origin and spread of lineages and communities; the origin of the northern temperate element within the Latin American biota; and the climatic and biotic consequences of the rise of the Andes Mountains, the opening of the Drake Passage between Antarctica and South America, and the closure of the Isthmus of Panama. Another consideration in formatting the coverage was to select topics and develop a sequence of presentations that would provide a logical unfolding of a complicated history for both specialists and the general reader. The companion volume on North America has been used for upper-division undergraduate and graduate-level courses and seminars, and the present text has been designed for the same purpose. To achieve the goal of reference manual and a general text, many of the data and supporting details are presented in tables and placed in appendices at the end of the book. There is a detailed subject index, and a section on General Readings with updates is included in the References at the end of each chapter.

The survey begins with background summaries on the geography (Chapter 1), geology (Chapter 2), and vegetation (Chapter 3). The geographic definition of the region is comparatively straightforward—it is Latin America and it extends from about 32°N, south across the Tropic of Cancer at 23.5°N and the Tropic of Capricorn at 23.5°S (the geographic tropics), to about 55°S. A more formal definition of Latin America as a political region is given in Chapter 1. This coverage provides reference points and place names for geologic features, vegetation types, and fossil localities mentioned in the text, and it follows the organization of the earlier volume on North America north of Mexico. There are several useful Web sites for additional geographic information on Latin America. These change frequently, but among those operational at the time of writing are http://earth.google.com (allows tilting of aerial view relief maps [DEM—Digital Elevation Models] to give topographic profiles), http://earth-info.nima.mil/gns/html, and http://www.sasi.group.shef.ac.uk/worldmapper/index.html.

It is less easy to set a suitable time span for the geologic review, but the one emphasized here begins in the Late Cretaceous, about 70 Ma, when (1) the modern angiosperm flora had ecologically diversified and was established over much of the globe (Coiffard et al., 2007; Heimhofer et al., 2007), (2) many taxa were modern enough in aspect to allow identification of the fossils to the family and generic level, and (3) an increasing number of organisms were associated in plant formations sufficiently similar to extant ones to allow estimates of the paleoenvironment.

Just as the Late Cretaceous encompasses a watershed biological event in the rise to dominance of the angiosperms, it is also immediately prior to the asteroid impact at Chicxulub

on the Yucatán Peninsula of Mexico 65 million years ago. The impact was cataclysmic, and the history of the modern communities in the Caribbean region begins with the recovery biota at the Cretaceous/Tertiary boundary. The impact left an enduring legacy on the Yucatán carbonate platform by creating a ring of cenotes (sinkholes) that presently encircle the crater, and that later would play a central role in the development of the lowland Maya civilization and the preservation of their artifacts. Evidence is also emerging for a possible impact effect on the biotas of the Southern Hemisphere (Chapter 7). The record of vegetation and associated geologic events is a continuum, but the Late Cretaceous is a convenient starting point for tracing the history of the modern angiosperm-dominated flora. The Late Cretaceous to Recent also corresponds to the interval covered in the companion volume on North America north of Mexico. The synopsis of the geology of Latin America presented in Chapter 2 focuses on land-sea relationships, mountain uplift, the movement of terranes and volcanic island arcs from which much of Latin America was constructed, and on sedimentary clues to past environments and events that affected the vegetation. Chapter 3 is a summary of the modern plant formations of Latin America, edited into a new classification of Latin American vegetation at the formation level consistent for the region and suitable for paleovegetation analysis. Appendix 1 is a listing of these formations with representative species. These three chapters on Geography, Geology, and Vegetation constitute Section I (Background), and they are intended to level somewhat the subject terrane over which readers with different backgrounds and interests will progress.

The principal fossil floras and the terrestrial paleoenvironments for Latin America are presented in Section II (The Database). Studies prior to about 1960, and now mostly out-of-date, were based exclusively on plant megafossils, while the post-1960 literature includes studies of rodent middens, spores, pollen, diatoms and other algae, starch grains, and phytoliths. A considerable part of the record by necessity is based on microfossil assemblages, although a number of important Late Cretaceous and Cenozoic megafossil floras are now under study and a greater balance is being achieved. Even so, conditions suitable for their preservation are not commonplace, especially in tropical environments (Prologue Fig. 1). Chapters 4–7 of Section II discuss representative Late Cretaceous and Cenozoic fossil floras of Mexico (with taxa listed in Table 4.1), the Antilles (Table 5.1), Central America (Table 6.1), and South America (Table 7.1–Cretaceous and Paleogene floras; 7.2–Neogene floras; and 7.6–Quaternary floras). The taxa from all the tables are arranged by age in Appendix 2.1 and by plant group or family in Appendix 2.2. The latter index is likely to be the one of greatest interest to those seeking to compile the geologic record of a particular lineage. It is possible to read the text and search the tables and appendices in the sequence presented. It is also possible to read sections of chapters for the paleobotanical record of a country or region, a segment of geologic time, or the occurrence and stratigraphic range of a particular morphotype, lineage, or community. Combined with

Prologue Figure 1. Deterioration of a tropical leaf by fungi and bacteria, and colonization by lichens and mosses. These processes affect the preservability of megafossils in tropical regions. From Richards (1996). Reprinted with the permission of Cambridge University Press.

the index and tables in the earlier volume, a record is available for most of the Late Cretaceous and Cenozoic fossil plants of the New World. With this database it is possible to address broader topics involving multiple regions and spans of time, and these are discussed in Section III (Syntheses).

The effective use of the vast paleobotanical and geological literature presents a special challenge. Many identifications of plant megafossils made early in the century are questionable, and many plant microfossils were studied primarily for purposes of stratigraphic correlation and named by an artificial system in which establishing biological affinities was attempted with various levels of commitment and a wide range of success. This limits their value, but the names are in the literature, nonetheless, and are used by scientists working in other fields. To address the uneven availability and reliability of the data, the geological coverage emphasizes recent summaries and tectonic models around which some consensus is developing. The paleobotanical citations and plant fossil records are more inclusive, but incorporate recent changes in age assignments and references to studies where identifications have been questioned, confirmed, or revised.

Electronic databases dedicated to vegetation history and related topics at present are only partly developed and inconsistently maintained. It is possible to make general literature searches through BioAbstracts, BioOne, GeoRef, Institute of Scientific Information (ISI), Web of Science, WorldCat, and other search engines and, by using the "combine" format, to focus on specific topics (e.g., "Quaternary + sea-level change + the Antilles"). Retrieval of reports of individual taxa (e.g,

Rhizophora) or paleocommunities (mangroves) is more difficult because this requires multiple, often language-specific key words (e.g., mangrove and manglar), no one compilation is complete, databases are often compiled for either microfossils or megafossils, several are geographically defined (e.g., Africa, southeastern Asia), and none are fully linked to give a complete search. Searchable electronic catalogs are the expected norm in modern science, they are clearly the method of the future, and they need to be better developed in the field of paleobotany.

Some examples of databases are those on modern spore and pollen types at the Florida Institute of Technology (http://research.fit.edu/bushlab/pollen_db.htm); the NOAA-National Geophysical Data Center world pollen and spore database (http://www.ngdc.noaa.gov/paleo/pollen.html); Spores and pollen of Barro Colorado Island, Panama (http://striweb.si.edu/roubik); and the University of Vienna (http://paldat.botanik.univie.ac.at/). The University College of London is developing MIRACLE (Microfossil Image Recovery and Circulation for Learning and Education [http://www.ucl.ac.uk/GeolSci/micropal/palynology.html]). The International Organization of Palaeobotany (IOP) initiated the Plant Fossil Record (Boulter et al., 1991; Holmes, 1991; http://www.UK-bap.org.uk and http://www.paleobotany.org) to provide data on plant micro- and megafossils. The project is now moribund, and it needs to be reactivated. Reconstructing the fossil record of a lineage is presently a lengthy and complicated process. Until electronic libraries are more advanced, the process begins with personal communications with specialists, involves collaborative studies, and requires consulting traditional compilations.[1] The latter include Hulshof and Manten (1971) and Tissot and van der Ham (1994) on modern spore and pollen morphology; illustrations of modern spore and pollen types as part of taxonomic studies (e.g., Dessein et al., 2005, Rubiaceae; McDade et al., 2005, Acanthaceae), and standardly included, for example, in the *Flora Neotropica* series from NY; the bibliographies on *Vegetation and Vegetational History of Latin America* (Graham, 1973, 1979, 1982, 1986), and other bibliographies cited therein under General Bibliographic References (see also Selected References on the Pollen Morphology of Predominately Neotropical Taxa); *Bibliografia Paleobotanica Argentina* (Archangelsky et al., 2000); Bibliography of American Paleobotany (Paleobotanical Section, Botanical Society of America); and the *Review of Palaeobotany and Palynology*'s Bibliography and Subject Index (1998) and Bibliography of Palaeopalynology 1836–1966 (1969). Compilations of the older literature are provided in Andrews (1970, supplements 1975, 1982), LaMotte (1952), and Muller (1981). Other catalogs and bibliographies for specific countries and regions are mentioned at appropriate places in the text.

A geologic timescale is presented on the inside front cover (Palmer & Geissman, 1999; Gradstein et al., 2005; Berggren et al., 1995; also see the Earthtime Web site [http://www.earthtime.org]; see also I: p. x). With reference to radiometric ages cited for the Quaternary, uncalibrated ^{14}C years are approximately 2000 years too young for material older than 12,500 years, and 250–500 years too young for more recent material because the amount of radiocarbon in the atmosphere has varied over time. It is possible to calibrate the ^{14}C clock by comparing the ages with independently derived dates such as tree rings back to ~11,800 years (e.g., CALIB 3.0; Stuiver & Becker, 1993; Stuiver & Reimer, 1993; Guilderson et al., 2005). The INTCAL04 ^{14}C curve extends back to 26,000 years (Bard et al., 2004), and it may soon be possible to date materials as old as 50,000 years (the practical limit of the technique; Hughen et al., 2004; see also *Science*, 2005, Vol. 308: 51–53). In the current literature, dates are typically given as calendar years B.P. (before present; i.e., ^{14}C-calibrated), ^{14}C years (uncalibrated), or for more recent material B.C. (before Christ), A.D. (anno domini), C.E. (common era), or B.C.E. (before the common era). Unless otherwise stated, dates in the text for the Quaternary are calendar years (for a discussion of U-Th dating see Placzek et al., 2006, pp. 517–518).

Abbreviations and symbols are explained the first time they are used in the text, and under Nomenclature at the end of the Prologue. In the References, all authors are cited up to five, and beyond that et al. is used [e.g., Balmford, A. et al. (+ 18 authors)]. Chapters, figures, appendices, and tables cited in uppercase (e.g., Chapter 1) refer to the present text, and those in lowercase refer to those in other publications.

The spelling of scientific names and family assignments for modern plants have been checked using TROPICOS (MO; http://www.tropicos.org). Nomenclature for modern ferns follows Tryon and Tryon (1982), recognizing that revisions in family classification and generic arrangements are actively under way. In the tables and appendices, fern taxa are listed alphabetically by genus, rather than by family, following the system at Missouri Botanical Garden (MO). The age of the fossil floras is given according to the original authors, along with revised updates. The names, spellings, and family assignments of the fossil plants assigned to modern taxa present a special problem. An updated nomenclature is presented based on TROPICOS, but the original spellings are also provided. This is because if records from the early paleobotanical literature are faithfully databased, searches, for example, for *Annona* and *Byttneria* (current spellings), will be incomplete because in much of that literature they are rendered *Anona* and *Buettnaria* or *Buttneria*. These inconsistencies, the varied family assignments, and altered modern taxon distributions resulting from taxonomic revisions (e.g., *Bombax* and *Engelhardia* are no longer New World genera) will have to be addressed in databasing paleobotanical records involving modern plant names.

Although much of the factual information upon which vegetation history is based can be verified, the generalizations and concepts derived from that information are continually being revised. Past experience has demonstrated that reaction to new methodologies and innovations, including evolution, plate tectonics, vicariance, molecular systematics, and cladistics, often involve an initial period of pointed rejection or enthusiastic advocacy, a less understandable period of demeaning established and complementary approaches, and eventually one in which

the novel discipline takes its place as one of many sources of information about complex phenomena. Several facets of vegetation and environmental history are in the midst of these dialogues, and my views about some of them are presented as Cautionary Notes and Opinions (nomenclature, identifications, "fern spikes," narrative biogeography, assessing the plant fossil record, molecular clocks, and refugia). Among the problems created by presenting opinions as proclamations and defending positions against mounting evidence to the contrary are (1) it contributes little to the discipline, (2) it delays achieving better knowledge of the subject, and (3) although often good theater, it is a poor instructional model.

An improved understanding of tropical biotas and environments is being gained by garnering information from the study of individual floras, combining it with results from faunal studies to reconstruct biotic histories, and incorporating this information with data on physical and climatic environments to achieve a knowledge of ecosystem evolution. It will be argued in the pages to follow that the ecosystem stage is reached when history is seamlessly incorporated with neobiology in envisioning biotas. From that knowledge, the wisdom may emerge for conceptualizing the origin, diversification, radiation, and functioning of the Earth's biota, as well as for developing a rational stewardship of its resources (Willis et al., 2007). However, one thing is certain—that wisdom will never emerge without the historical component and the integration of information from the widest range of disciplines. The equatorial regions are critical because they are part of a functioning global ecosystem and because of all things that live, two-thirds live in the tropics. The fact that we are nearing a point where five centuries of study and exploration are beginning to provide the necessary clues is immensely satisfying. If we agree that a concern for the quality of life we are forging for future generations is a legitimate part of the human spirit, then seeking knowledge of where we have been is worthwhile because it gives a more realistic assessment of present conditions, and a clearer indication of where we are heading. In the middle Pliocene, 4 million years ago, the biota lived on an Earth that was ~3.5° C warmer than at present—the temperature expected to be reached again in about 200 years. At the end of the last major glacial advance 11,000 to 12,000 years ago, the CO_2 concentration of the atmosphere was about 260 parts per million by volume (ppmv). Since then, and especially after the Industrial Revolution beginning in the early 19th century, it began to rise more rapidly, reaching 300 ppmv, then after World War II 320 ppmv, and now 378 ppmv. If present trends continue, it will reach an estimated 500 ppmv in 2050, and 700–1000 ppmv toward the end of this century. Analogs for these values and the biota they supported are available from the past. Based on carbon isotopic values of di-unsaturated alkenones in deep sea cores, "pCO_2 ranged between 1000 to 1500 [ppmv] in the middle to late Eocene, then decreased in several steps during the Oligocene, and reached modern levels by the latest Oligocene" (Pagani et al., 2005).

In a lecture at E. J. Thomas Hall in Akron, Ohio (14 November 2000), historian David McCullough, paraphrasing former U.S. Librarian of Congress Daniel Boorstin, noted that "trying to understand the present [or anticipate the future] without knowing the past is like trying to plant a garden with cut flowers." This text provides a foundation for understanding one aspect of that past—the history of vegetation and terrestrial environments in Latin America. It begins with a description of the Lay of the Land.

Prologue Figure 2. Photograph of a fossil specimen of *Oreopanax precoccinea* (aff. *O. floribunda* group) incorporated into the University of Michigan Herbarium. From Graham (1962). Used with permission of *Taxon* (International Association of Plant Taxonomists).

NOTES

1. In an early effort to further cooperative studies between paleobotany and taxonomy, I began a project at the University of Michigan of mounting photographs of fossil plants on herbarium sheets, with data on identification, age, locality, and pertinent literature, and inserting these into the folders of the most similar living species (Graham, 1962; Prologue Fig. 2). The initial example was a specimen of *Oreopanax precoccinea* (Brooks) Arnold from the Miocene Succor Creek flora of Oregon. The generic identification was confirmed by taxonomist José Cuatrecasas (US) who further suggested the *O. floribunda* group as the nearest living relatives. Among the anticipated advantages to paleobotanists were continuing assessments by taxonomists of the identifications and updates on the distribution and ecology of the modern analogs. The advantage to taxonomists would be an introduction to the fossil record of their particular group conveniently presented and easily assessed. Practical considerations and new technologies forestalled this approach, but some version of the effort, perhaps now as an electronic record, should be considered.

REFERENCES

Achard, F. et al. (+ 6 authors). 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297: 999–1002. [See also Comment, Fearnside and Laurance, Response, Eva et al., 2003, Science 299, 14 Feb.]

Andrews, H. N., Jr. 1970. Index of Generic Names of Fossil Plants, 1820–1965. U.S. Geological Survey Bull. 1300: 1–354. Supplements: A. M. Blazer, 1975. 1966–1973, Bull. 1396: 1–54. A. D. Watt, 1982. 1974–1978, Bull. 1517: 1–63.

Archangelsky, S., L. Lezama, and A. Archangelsky. 2000. Bibliografía Paleobotánica Argentina. Publicación Especial MEF (Museo Paleontológico Egidio Feruglio) No. 1. Trelew-Patagonia, Argentina. [Initial number in the series is by Carlos A. Menéndez, 1957.]

Balmford, A. et al. (+ 18 authors). 2002. Economic reasons for conserving wild nature. Science 297: 950–953.

Bard, E., F. Rostek, and G. Ménot-Combes. 2004. A better radiocarbon clock. Science 303: 178–179.

Berggren, W. A., D. V. Kent, M.-P. Aubry, and J. Hardenbol (eds.). 1995. Geochronology Time Scales and Global Stratigraphic Correlation. Society for Sedimentary Geology (SEPM), Tulsa. Special Publication 54.

Boulter, M. C., W. G. Chaloner, and P. L. Holms. 1991. The IOP plant fossil record: Are fossil plants a special case? *In:* D. L. Hawksworth (ed.), Improving the Stability of Names: Needs and Options. Regnum Vegetabile No. 123, Koeltz Scientific Books, Königstein, Germany. pp. 231–242.

Coifford, C., B. Gomez, and F. Thevenard. 2007. Early angiosperm invasion of western Europe and major environmental changes. Ann. Bot. 100: 545–553.

Dessein, S. et al. (+ 8 authors). 2005. Palynological characters and their phylogenetic signal in the Rubiaceae. Bot. Rev. 71: 354–414.

Gradstein, F. M., J. Ogg, and A. Smith. 2005. A Geologic Time Scale 2004. Cambridge University Press, Cambridge, U.K.

Graham, A. 1962. Paleobotany and the university herbarium. Taxon 11: 218–220.

———. 1973. Literature on vegetational history in Latin America. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 315–360.

———. 1979. Literature on vegetational history in Latin America. Supplement I. Rev. Palaeobot. Palynol. 27: 29–52.

———. 1982. Literature on vegetational history in Latin America. Supplement II. Rev. Palaeobot. Palynol. 37: 185–223.

———. 1986. Literature on vegetational history in Latin America. Supplement III. Rev. Palaeobot. Palynol. 48: 199–239.

Guilderson, T. P., P. J. Reimer, and T. A. Brown. 2005. The boon and bane of radiocarbon dating. Science 307: 362–364.

Heimhofer, U., P. A. Hochuli, S. Burla, and H. Weissert. 2007. New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: Implications for the timing of the early angiosperm radiation. Rev. Palaeobot. Palynol. 144: 39–76.

Holmes, P. L. (ed.). 1991. The plant fossil record database, version 1.0. International Organization of Palaeobotany, London.

Hughen, K. et al. (+ 6 authors). 2004. ^{14}C activity and global carbon cycle changes over the past 50,000 years. Science 303: 202–207.

Hulshof, O. K. and A. A. Manten. 1971. Bibliography of actuopalynology 1671–1966. Rev. Palaeobot. Palynol. 12: 1–243.

LaMotte, R. S. 1952. Catalogue of the Cenozoic Plants of North America through 1950. Geol. Soc. Amer. Mem. 51: 1–381.

Leshner, A. 2002. Science and sustainability. Science 297: 897.

Mann, C. C. 2002. The real dirt on rainforest fertility. Science 297: 920–923. [See also inset, The Forgotten People of Amazonia.]

McDade, L. A., T. F. Daniel, C. A. Kiel, and K. Vollesen. 2005. Phylogenetic relationships among Acantheae (Acanthaceae): Major lineages present contrasting patterns of molecular evolution and morphological differentiation. Syst. Bot. 30: 834–862.

Morton, O. 2005. Specks of evidence from ancient sunburn. Science 309: 1321.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47: 1–142.

Pagani, M., J. C. Zachos, K. H. Freeman, B. Tipple, and S. Bohaty. 2005. Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. Science 309: 600–603.

Palmer, A. R. and J. Geissman (compilers). 1999. 1999 Geologic Time Scale. Geological Society of America, Boulder, CO.

Placzek, C., J. Quade, and P. J. Patchett. 2006. Geochronology and stratigraphy of late Pleistocene lake cycles on the southern Bolivian Altiplano: Implications for causes of tropical climate change. Geol. Soc. Amer. Bull. 118: 515–532.

Raven, P. H. 2002. Science, sustainability, and the human prospect. Science 297: 954–958.

Review of Palaeobotany and Palynology. 1969. Special volume, Bibliography of Palaeobotany 1836–1966. Vol. 8: 1–570.

———. 1998. Bibliography, Vols. 51–100. Rev. Palaeobot. Palynol. 100: 125–187.

Richards, P. W. (with contributions by R. P. D. Walsh, I. C. Baillie, and P. Greig-Smith). 1996. The Tropical Rain Forest, 2nd ed. Cambridge University Press, Cambridge, U.K.

Stuiver, M. and B. Becker. 1993. High-precision calibration of the radiocarbon time scale A.D. 1950–6000 B.C. Radiocarbon 35: 35–65.

——— and P. J. Reimer. 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. Radiocarbon 35: 215–230.

Tissot, C. and R. van der Ham. 1994. Seventh bibliographic index to the pollen morphology of angiosperms. Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry 27: 1–345.

Tryon, R. M. and A. F. Tryon. 1982. Ferns and Allied Plants with Special Reference to Tropical America. Springer Verlag, Berlin.

Willis, K. J., L. Gillson, and S. Knapp (Organizers and eds.). 2007. Biodiversity hotspots through time: Using the past to manage the future. Papers of a Theme Issue. Philos. Trans., Ser. B 362: 167–333.

ADDITIONAL REFERENCES/GENERAL READINGS/ ELECTRONIC ADDRESSES

American Association of Stratigraphic Palynologists (AASP). http://www.palynology.org.

Anonymous. 2001. Make the most of Palaeodata. Nature 411: 1.

Asociación Latinoamericana de Paleobotánica y Palinología. http://www6.ufrgs.br/alpp.

Chittenden, D., G. Farmelo, and B. V. Lewenstein (eds.). 2004. Creating Connections: Museums and the Public Understanding of Research. AltaMira Press, Walnut Creek, CA. [Review in Nature 2004, Vol. 431: 743.]

Culotta, E. 1993. Is the geological past the key to the (near) future? Science 259: 906–908.

Generic Mapping Tools. http://www.aquarius.ifm-geomar.de/.

International Federation Palynological Societies (IFPS). http://www.geo.arizona.edu/palynology/index.html.

Kerr, R. A. 2003. A call for telling better time over the eons. Science 302: 375.

Merali, Z. and J. Giles. 2005. Databases in peril. Nature 435: 1010–1011.

Morris, D. M. and M. Z. Morris. 2002. English-Spanish Dictionary of Plant Biology: Including Plantae, Monera, Protoctista, Fungi and Index of Spanish Equivalents. Cambridge International Science Publishing, Cambridge, U.K.

Schrag, D. P. and R. B. Alley. 2004. Ancient lessons for our future climate. Science 306: 821–822.

Vrba, E. S., G. H. Denton, T. C. Partridge, and L. H. Burckle (eds.). 1995. Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, CT.

NOMENCLATURE

A.D.	anno domini
AMS	accelerator mass spectrophotometry
AP	aboreal (tree) pollen
ATB	Association for Tropical Biology
B.C.	before Christ
B.C.E.	before the common era
B.P.	before the present
CCD	calcite compensation depth
C.E.	common era (A.D.)
chenoam	Chenopodiaceae/Amaranthaceae (for pollen types mostly indistinguishable)
CLAMP	Climate-Leaf Analysis Multivariate Program
CLIMAP	Climate Long-Range Investigation and Mapping Program
COHMAP	Cooperative Holocene Mapping Project
c-t-t, TCT	Cupressaceae-Taxaceae-Taxoidaceae (pollen types mostly indistinguishable)
dbh	diameter at breast height
DEM	digital elevation model
D–O	Dansgaard–Oeschger events
DSDP	Deep Sea Drilling Project
EECL	Early Eocene Climatic Optimum
ELA	equilibrium line altitude—altitude on a glacier where mass balance equals zero, separating zones of accumulation and ablation (ref. Chapter 4, Basins of the Transvolcanic Belt and Vicinity)
ENSO	El Niño–Southern Oscillation
E/P	evapotranspiration
Ga	giga; billion years, billions of years ago
GCM	General Circulation Model
GIS	Geographic Information System
GPS	Global Positioning System
ha	hectare (= 2.47 acres)
IODP	Integrated Ocean Drilling Program
IOP	International Organization of Palaeobotany
ISI	Institute of Scientific Information
ITCZ	Intertropical Convergence Zone
K/T	Cretaceous/Tertiary boundary, approximately 65 Ma
Kyr	thousand years, thousands of years ago
LGM	Last Glacial Maximum (approximately 18,000 years B.P.)
LDD	long-distance dispersal
LMA	leaf margin analysis
LPTM	Late Paleocene Thermal Maximum
Ma	million years, millions of years ago
MAP	mean annual precipitation
MAT	mean annual temperature
(M)MCO	(Middle) Miocene Climatic Optimum
MIRACLE	Microfossil Image Recovery and Circulation for Learning and Education
MIS	marine isotope stage
MO	Missouri Botanical Garden
MPWI	mid-Pliocene warm interval
M_S	surface wave scale, one of three units of earthquake measurement (others M_L = Richter scale, M_b = body wave scale)
msl	mean sea level
mtDNA	mitochondrial DNA
NAP	non-arboreal (herbaceous) pollen
NSF	National Science Foundation
Neogene	Miocene and Pliocene
NLR	nearest living relative (modern analog method)
NY	New York Botanical Garden
OBFS	Organization of Biological Field Studies
ODP	Ocean Drilling Program
OIS	oxygen isotope stage
OSL	optically stimulated luminescence, a means of dating minerals and ceramics (last firing) vs. radiocarbon for organic material
OTS	Organization for Tropical Studies
PAGES	Past Global Change Project of the International Geosphere Biosphere Program (including PEP, Pole-Equator-Pole Transects, e.g., Americas transect, PEP1)
Paleogene	Paleocene, Eocene, and Oligocene
pCO_2	atmospheric carbon dioxide concentration
P/E	precipitation to evaporation
PEMEX	Petróleos de Mexicanos
PEP	(see PAGES)
PETM	Paleocene–Eocene Thermal Maximum
PGCO	Post Glacial Climatic Optimum
ppmv	parts per million by volume
PRISM	Pliocene Research Interpretation and Synoptic Mapping
RECOPE	Refinadora Costaricense de Petroleo
SASM	South American southern monsoon
STRI	Smithsonian Tropical Research Institute

SST	sea surface temperature(s)
TCT	Taxodiaceae-Cupressaceae-Taxaceae (pollen types mostly indistinguishable)
UC MEXUS	University of California Institute for Mexico and the United States (organization focusing on topics of concern to the U.S. and Mexico)
UNAM	Universidad Nacional Autónoma de México
US	United States National Herbarium, Smithsonian Institution
USNM	United States National Museum (of the Smithsonian Institution)
~	approximately

Several plant family names have changed from the original publications. The following are newer names used in the text, and older names included in the tables and appendices: Apiaceae-Umbelliferae; Arecaceae-Palmae; Asteraceae-Compositae; Brassicaceae-Cruciferae; Clusiaceae-Guttiferae; Fabaceae-Leguminosae; Lamiaceae-Labiatae; Poaceae-Gramineae; also *Pelliciera-Pelliceria.*

SECTION I

BACKGROUND

Geography • Geology • Vegetation

Chapter 1

LAY OF THE LAND

Climates and Physical Geography

"…for a transitory enchanted moment man must have held his breath in the presence of this continent, compelled into an aesthetic contemplation he neither understood nor desired, face to face for the last time in history with something commensurate to his capacity for wonder." (F. Scott Fitzgerald, *The Great Gatsby*)

The definition of Latin America varies according to the many organizations that classify the region for diverse scientific, political, economic, cultural, and defense purposes.[1] To standardize the different uses encountered in the literature, the terminology of SALA (Statistical Abstract of Latin America; Wilke, 1996) is followed, and it is augmented by Carlson (1952), Europa World Yearbook (1996), Famighetti (1997), and Hunter (1997). According to SALA, Latin America, as perceived by itself, consists of 20 countries, while Extended Latin America includes 27 additional political units such as territories, commonwealths, departments, and former colonies (Table 1.1). As used here, Latin America refers to Extended Latin America. Few generalizations can be made about the region because of its vast extent and diversity. The total area is ~20,532,960 km^2, or about twice the size of conterminous United States. It extends through 87° of latitude from northwestern Baja California at 32°N to southern Tierra del Fuego at 55°S. Elevations range from below sea level in the Cul-de-Sac/Enriquillo Basin region of Haiti and the Valdés Peninsula of southern Argentina (–13 m) to the highest peak in the Americas (Cerro Aconcagua, Argentina, 6960 m), one of 20 peaks in Latin America that exceed North America's tallest peak (Mt. McKinley, 6194 m, in Denali National Park, Alaska). The Amazon is the world's second-longest river, extending 6450 km through the lowlands of Brazil (but see http://earthobservatory.nasa.gov/IOTD/; possibly longest at 6800 km). The Nile River is the longest at 6670 km; the Yangtze is third at 6380 km. The Amazon is 4–5 km wide at its greatest width at the confluence with the Río Negro, and branches to 340 km where it discharges into the Atlantic Ocean around Marajó Island on the northwest coast of Brazil. The Amazon has the greatest discharge of any river at 175,000 m^3/sec, and it deposits 1000 million tons of silt into the ocean each year. Spellings and statistical information on these and other physical features follow *The Oxford Atlas of the World* (1997), *The Times Atlas of the World* (1995), and the U.S. Board on Geographic Names (1956 et seq.).

Some General Aspects of Climate

The range in climate in Latin America is as vast as the topography, even as recorded from the coastal and middle-elevation population centers for which the longest and most detailed records exist. For example, mean annual temperature (MAT) is 28.3° C at Choluteca, Belize, and 6.6° C at Punta Arenas, Chile. In remote areas for which climate data are often meager, temperatures, precipitation, and their annual ranges approach the extremes for the entire planet. Mean annual precipitation (MAP) varies from no measurable rain for extended periods at places in the Atacama Desert of northern Chile to ~11,000 mm (463 in) at Tutunendo (Department of Chocó) in northwestern Colombia.[2]

Climates are determined by a myriad of interacting factors and one of the most important is atmospheric circulation (I: pp. 28–44). One form of this circulation, known as the Hadley convection cell, operates primarily between latitudes 30°N and 30°S. The surface of the equatorial region is perpendicular to the sun throughout the year, while the curvature of the Earth increases obliquely toward the poles. This obliquity or slant results in a given amount of heat being dispersed over a larger area at the high latitudes than at the low latitudes. It also increases the distance through the atmosphere that the sun's rays must pass before reaching the Earth's surface, and this results in greater atmospheric absorption of heat. In addition, the tilt of the Earth's axis of 23.5° means that heat strikes the Earth at near right angles for progressively shorter periods of time toward the high northern and southern latitudes. The farthest points at which maximum insolation is received are at 23.5°N (the Tropic of Cancer; Fig. 1.1) and 23.5°S (the Tropic of Capricorn) and then only momentarily at times designated as the solstices (the longest/shortest days of the year, June 21 and December 21). These factors of angle, curvature, and tilt mean that the Earth's surface and lower atmosphere in the equatorial region is warmed more by insolation than at the poles. The warm air rises, cools, and begins to lose moisture when the

Figure 1.1. Monument marking the position of the Tropic of Cancer, the northern limit of the geographic tropics at 23.5°N, near Matehuala, San Luis Potosí, Mexico.

clouds reach an altitude of ~3000 m, and rainfall becomes heavy when they reach 5000–6000 m. On an idealized landscape, the equatorial zone would be characterized uniformly by warm temperature, low atmospheric pressure, extensive cloud cover, high rainfall, and tropical vegetation. The plant cover and clouds contribute to the maintenance of warmth by absorbing heat and reducing re-radiation, respectively. Vegetation further serves as a positive feedback to precipitation because in equatorial regions, transpiration returns ~75% of the rainfall back to the atmosphere, and ~50% of the precipitation over the rain forest is generated by the forest itself (Clapperton, 1993). At about 30°N and 30°S, this cooled dry air begins to descend and warms as it approaches the Earth's surface. Thus, conditions on an idealized landscape within these middle latitudes would be characterized uniformly by high temperatures, high atmospheric pressure, low rainfall, and desert vegetation. The Sonoran and Chihuahuan deserts of northern Mexico, and the dry Monte and Gran Chaco of Argentina and adjacent regions exist, in part, because they are located in a persistent high-pressure zone beneath the descending arm of the Hadley convection cell. However, the idealized distribution of tropical and temperate zones implied by the Hadley atmospheric circulation pattern is greatly modified by the moisture transport of atmospheric currents and the heat transport of ocean currents, and both are influenced by topography.

Atmospheric currents

As air descends, the spinning motion of the Earth produces air currents (Coriolis Effect). These directional flows of air are called the easterlies (viz., from the east), westerlies, and trade winds (Fig. 1.2), and they are an important factor in determining the climates of Latin America. The northeast trade winds define the hurricane tracts that are a source of moisture for the Caribbean Basin and the Atlantic and Amazon rain forests of Brazil. In contrast, the westerlies, after crossing the cold waters of the Humboldt Current, arrive on the west coast of South America as a moisture-depleted, desiccating wind that contributes to the arid conditions of the Atacama Desert of Chile.

To the north and south of latitudes 30°, the Hadley regime gives way to a different form of atmospheric circulation—two to five superimposed waves moving eastward at 50–100 km/hr called the Rossby regime. Within these westerlies, there are cores of air moving at 150–300 km/hr called the jet streams. During the boreal (Northern Hemisphere) and austral (Southern Hemisphere) winter months, when the respective hemispheres are tilted away from the sun, shifts in the jet streams periodically bring cold air deep into the middle and lower latitudes (e.g., the nortes of northern Latin America; the pamperos of Argentina). Shifts in the position of the jet streams are limited by the warm northeast and southeast trade winds originating in the persistent high-pressure systems at 30°N and 30°S. The strength of the trade winds is greatest during the warm months and brings the moisture of the rainy season. When the flow of the trade winds weakens in the winter months, this produces the characteristic dry season. It is the weakening of the trade winds that further allows the polar incursion of cold air into the geographic tropics, from the north as far as Costa Rica, and from the south to central Argentina and beyond (polar air outbreaks; Marengo & Rogers, 2001). These incursions can lower temperatures by 6°–7° C in a few hours and produce brief local frost. Even the tropical lowlands of equatorial Brazil can be affected:

> "There is, in the month of May, a short season of very cold weather, a most surprising circumstance in the otherwise uniformly sweltering climate. This is caused by the…cold wind, which blows from the south over the humid forests…the temperature is so much lowered that fishes die in the river…the wind is not strong; but it brings cloudy weather, and lasts from three to five or six days in each year…the period during which this wind prevails is called the tempo da friagem or season of coldness." (Bates, 1930, pp. 293–294, quoted from Blouet & Blouet, 1993)

The north and south trade winds meet just north of the

equator at the Intertropical Convergence Zone (ITCZ). This is a climatically important region of complex weather instability and, in addition to the convection cell of the Hadley regime, seasonal shifts in the ITCZ are a major factor in determining the rainfall and precipitation patterns across the broad equatorial region (Martínez et al., 2006; Peterson & Haug, 2006; Poveda et al., 2006). From the Pacific Ocean, for example, irregular waves of high rainfall are conveyed eastward by the westerlies. During non-El Niño years, much of the moisture dissipates while blowing across the Humboldt Current and never reaches the coast. In El Niño years, the easterlies weaken and this allows the moisture-rich westerlies to reach the coast, and during extreme El Niños, as in 1982 and 1998, the Atacama Desert is converted into a lake-dotted flower land. One effect of a substantial increase in the frequency and/or intensity of El Niños would be to favor a shift from desert and shrubland to more persistent woodlands along the coastal desert (Holmgren et al., 2001). Although the relationship is not well understood, the strength of El Niños appears to be increasing with global warming. If so, they should have been prominent during warm periods of the past such as in the Miocene Climatic Optimum (MCO), mid-Pliocene warm interval (MPWI), and the interglacials. Long-term oscillations in the position of the ITCZ (e.g., during the warm versus cold periods of the Quaternary) would also create cyclic changes of rainfall in different parts of the Amazon Basin (Chapter 8, Refugia).

Along the Atlantic coast the northeast trade winds blow moisture across the Amazon Basin and, together with rain from the ITCZ, the ascending arm of the Hadley atmospheric circulation cell, and evaporation from the rain forest, they provide heavy precipitation. During non-El Niño years, hurricanes also bring immense amounts of water, including such notable examples as "the Great Hurricane" of 1831 that killed more than 1500 people on the island of Barbados; Gilbert (1988) with winds up to 210 mph that devastated the Yucatán Peninsula of Mexico; Andrew (1992) with winds 164–177 mph; Floyd (1999), which was one of the fiercest atmospheric disturbances ever recorded in the Atlantic Ocean; and Katrina (2005) with winds of 140 mph. Areas not directly in the path of the hurricanes can be severely affected, nonetheless, by torrents of rain such as the unrelenting amounts that fell for weeks across central Mexico in October 1999. One result of global warming during the past decades has been a 5%–10% increase in hurricane wind velocity in the Caribbean region. There were presumably similar increases during warm periods of the geologic past, and decreases during cooler intervals.

Hurricanes create gaps in the forest canopy, and these are important in tropical forest dynamics (see Fig. 1.12). In the Dr. Alfredo Barrera Marín Botanical Garden (Quintana Roo, Mexico) after Hurricane Gilbert, tree density decreased by 33%, basal area by 12%, height of trees in the lower canopy by 6%, those in the upper canopy by 12%, the understory by 51%, and ground cover by 70% (Sánchez & Islebe, 1999). In addition to the direct destructive effect, the open ground is initially populated by grasses and other herbs, making the openings

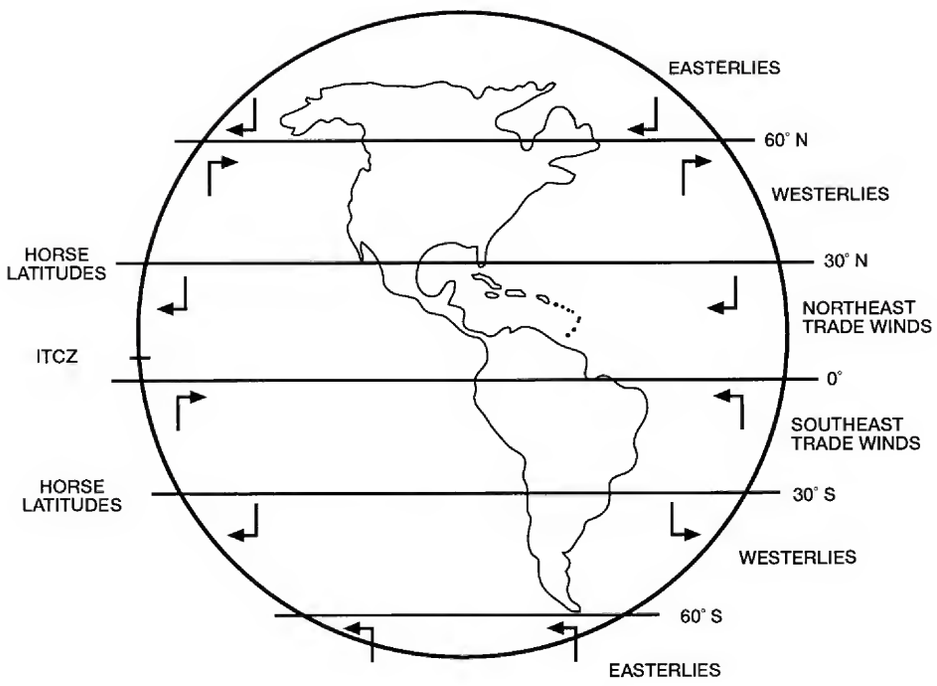


Figure 1.2. Schematic representation of wind directions.

susceptible to ground fires from lightning, volcanism, and human activities that prolong the new grassy areas (see Chapter 5, the Antilles). Calsbeek and Smith (2003) suggest that recolonization of *Anolis* lizards by overwater dispersal, after population decreases from severe storms, is an important evolutionary mechanism in the group. If hurricane frequency and intensity increase with global warmth, and if hurricanes are a mechanism for *Anolis* evolution, it would be interesting to examine molecular evidence for peaks in diversification following warm intervals of the past (viz., at ~3.5 Ma, and on the 100-Kyr cycles of the Milankovitch variations for the past ~2 Ma).

During El Niño years, there are about one-tenth the number of hurricanes in the Caribbean, and the Amazon Basin then experiences extreme dryness. In the strong El Niño of 1998, there was little rain and extensive forest fires burned across Amazonia. The fires were visible from the Mir space station and affected air quality as far north as Toronto, Canada. An Associated Press release for 3 May 1998 noted that no rain had fallen in northeastern Brazil for more than six months. Heavy smoke provides a feedback to drought by interfering with cloud formation (i.e., by creating small moisture droplets that rise rather than fall; Andreae et al., 2004; Koren et al., 2004). Among the less publicized consequences of El Niños is the "Drought Industry" (Glantz, 2001), wherein some landowners accumulate property from impoverished farmers forced to sell at below market prices. A counter response has been the Landless Rural Workers' Movement, which has endorsed looting of government warehouses as a tactic of last resort to secure food, followed by intensification of efforts to protect property, retaliation, and escalation.

Ocean currents

A second factor modifying the idealized arrangement of climate zones is ocean circulation. The vertical and horizontal circulation of marine water results from differences in temperature and salinity densities, surface currents further reflect wind patterns, and all are modified by ocean floor topography, the position of continents, the configuration of coastlines, and

Table 1.1. Latin America and Extended Latin America as defined by Statistical Abstract of Latin America (SALA; Wilke, 1996). Rank is among the countries of Latin America; population density is the number of inhabitants per km^2 (1 = lowest). Capital cities and their population, and largest city if different from the capital, are listed under the name of each country.

The 20 Countries of Latin America

	Area	Population	
	km^2/rank	Number/ rank	Density/ rank
Argentina	2,776,889/2	32,713,000/4	12/3
Buenos Aires		11,580,000	
Bolivia	1,098,581/6	8,000,000/11	7/1
La Paz		1,320,000	
Brazil	8,511,965/1	153,322,000/1	18/5
Brasília		1,803,478	
Rio de Janeiro/São Paulo		18,420,000	
Chile	756,945/8	13,386,000/7	18/7
Santiago		4,700,000	
Colombia	1,138,914/5	33,613,000/3	30/10
Bogotá		5,590,000	
Costa Rica	51,100/17	2,717,000/19	60/15
San José		1,040,000	
Cuba	110,861/13	10,336,000/9	97/17
Havana		2,090,000	
Dominican Republic	48,734/18	7,313,000/12	150/18
Santo Domingo		2,200,000	
Ecuador	283,561/10	12,000,000/8	38/13
Quito		1,100,000	
Guayaquil		1,738,000	
El Salvador	21,041/20	5,376,000/14	256/20
San Salvador		1,051,000	
Guatemala	108,889/15	9,467,000/10	87/16
Guatemala City		2,183,000	
Haiti	27,750/19	6,625,000/13	239/19
Port-au-Prince		460,000	
Honduras	112,088/14	5,265,000/15	47/12
Tegucigalpa		520,000	
Mexico	1,958,201/3	87,836,000/2	45/14
Mexico City		19,370,000	
Nicaragua	130,000/12	3,999,000/17	31/6
Managua		1,148,000	
Panama	75,517/16	2,466,000/20	33/11
Panama City		1,175,000	
Paraguay	406,752/9	4,397,000/16	11/2
Asunción		1,270,000	
Peru	1,285,216/4	21,998,000/5	17/4
Lima		6,500,000	
Uruguay	177,414/11	3,112,000/18	18/9
Montevideo		1,363,000	
Venezuela	912,050/7	20,226,000/6	22/8
Caracas		3,960,000	

The 27 Additional Political Units of Extended Latin America

Independent

	Area in km^2	Population
Antigua-Barbuda	442	65,000
St. John's		
Bahamas	13,939	269,000
Nassau		
Barbados	430	260,000
Bridgetown		
Belize	22,965	205,000
Belmopan		
Dominica	750	71,000
Roseau		
Grenada	378	92,000
St. George's		
Guyana	214,969	816,000
Georgetown		
Jamaica	10,991	2,411,000
Kingston		
St. Kitts-Nevis	261	42,000
Basseterre		
St. Lucia	616	139,000
Castries		
St. Vincent/Grenadines	389	110,000
Kingstown		
Suriname	163,000	414,000
Paramaribo		
Trinidad and Tobago	5,128	1,260,000
Port of Spain		

Dependent

	Area in km^2	Population
Aruba	193	69,000
Oranjestad		
Anguilla	155	9,000
The Valley		
Bermuda	54	63,000
Hamilton		
British Virgin Islands	153	18,000
Road Town		
Cayman Islands	259	29,000
George Town		
French Guiana	91,000	135,000
Cayenne		
Guadeloupe	1,780	413,000
Basse-Terre		
Malvinas (Falkland Islands)	12,170	2,000
Stanley		
Martinique	1,079	371,000
Fort-de-France		
Montserrat	100	11,000
Plymouth		
Netherlands Antilles	800	195,000
Willemstad		
Puerto Rico	8,897	3,620,000
San Juan		
Turks and Caicos	430	13,000
Grand Turk		
U.S. Virgin Islands	344	104,000

land bridges. Ocean circulation distributes warm equatorial and cold polar waters through the Earth's ocean basins resulting in a more uniform distribution of heat, and currents along continental margins or through island chains are a factor in determining local to regional climates. The warm Gulf Stream is ~60 miles wide, flowing to a depth of 1000 m, and transports ~30 million m^3 of sea water through the Florida Straits each second. This displaces climatic zones northward and accounts for tropical corals growing as far north as Bermuda at 33°N, or about the latitude of Wilmington, Delaware.

Topography

Topography is a third factor that alters the idealized arrangement of climatic and biotic zones. Topographic features such as mountains, plateaus, and high masses of continental ice affect the amplitude, seasonal meandering, and direction of the jet streams by orographic deflection. It is estimated that at the glacial maxima the Laurentian and Cordilleran ice sheets of North America were ~1 mile in height. This split the polar jet stream and displaced the southern arm southward and replaced the high-pressure system over the southwestern United States and northern Mexico with a low-pressure system. The result was increased rainfall (pluvial climates) in the Mojave, Sonoran, and Chihuahuan deserts and replacement of the arid vegetation by shrubland/chaparral–woodland–savanna during each of the 18–20 glacial climates that constituted ~90% of the Quaternary period (i.e., 90,000 years of the 100,000-year Milankovitch eccentricity cycle). The familiar arid conditions and desert vegetation of the present interglacial are characteristic of only ~10% of the past 1.8 Ma.

Another consequence of topography is temperature gradients (lapse rate)—the change in temperature with latitude and altitude. MAT decreases with altitude at a world average gradient of 5°–6° C/km, and this affords a method whereby paleoelevations may be calculated from estimates of MATs based on fossil floras from low versus high altitudes (I: pp. 207–210). Temperature gradients are also used to estimate paleotemperatures of altitudinal zones from highlands into the lowlands (e.g., nival, super páramo, grass páramo, subpáramo, upper Andean forest, subandean forest; see Fig. 3.134). Where paleobotanical evidence from upland bogs or lakes indicates a vertical shift in these zones, the use of gradients allows a calculation of the temperature change. For example, if the lower limit of the subandean forest belt shifted downward by an estimated 1000 m at the glacial maxima, and a gradient of 5° C/km is assumed, then temperatures at 200 m in the lowlands would be ~5° C cooler than at present.

However, the gradient varies with local conditions. MAT at Mazatlán, Mexico, at an elevation of 78 m is 23.5° C, and at Zacatecas, Mexico, at an elevation of 2611 m it is 13.3° C for a temperature gradient of 4.1° C/km. From Maracaibo, Venezuela (near sea level, MAT 28.5° C), to Mérida, Venezuela (1700 m, MAT 18° C), the gradient is 6.0° C/km. A further complication is the Massenerhebung effect—the extension of similar vegetation zones to higher elevations on larger mountains than on smaller ones (Grubb, 1971). On major ranges, the upper limit of the lowland rain forest is ~1200–1500 m, and for the lower montane rain forest it is 1800–2300 m. On smaller ranges, the figures are 700–900 m and 1200–1600 m, respectively. The gradient is generally steeper below the condensation level (the cloud base) than above it. Bush and Silman (2004) discuss other complications in calculating past cooling and precipitation in the lowland tropics. There are broad ranges in the estimates of elevation and temperature based on paleobotanical data, but they provide approximations that can be refined by comparison with independent evidence (e.g., noble gases, isotopes in corals; Chapter 7, Quaternary). Collectively, the various lines of inquiry indicate a 5°–6° C lowering of temperatures for the Amazon lowlands at glacial maxima.

Topography also affects the amount and regional distribution of rainfall. In northern Latin America, winds blowing inland from the Atlantic Ocean provide rain to the coastal regions. As the wind rises and cools upon ascending the east-facing slopes of the Sierra Madre Oriental of Mexico, for example, there is even greater rainfall, or advective precipitation increases, in the mid-altitude highlands. Annual rainfall is 1613 mm at the coastal city of Veracruz and 2162 mm at Orizaba (elevation 1247 m), only 100 km apart. The relatively flat islands of Aruba, Bonaire, and Curaçao (the ABC Islands or Netherlands Antilles), off the northern coast of South America, receive ~508 mm of annual rainfall, while mid-elevation sites on the more topographically diverse island of Dominica receive more than 2540 mm. When moisture-laden winds blowing across the Amazon Basin ascend the east-facing slopes of the Andes Mountains and winds off the Pacific Ocean north of the Humboldt Current blow inland, large amounts of rain are produced. As noted previously, the Chocó region of Colombia is one of the wettest places on Earth with annual rainfall occasionally near 11,000 mm. During the austral summer months (December through March), the advected air produces ~80% of the MAP on the dry Altiplano of Bolivia. This moisture system involving the Atlantic Ocean–Amazon lowlands–eastern Andean slopes–Andean highlands is called the South American summer monsoon (SASM). Factors that affect its position or intensity, such as the atmospheric and ocean temperature fluctuations that occurred during the Quaternary, become forcing mechanisms for vegetation change. The interacting factors are immensely complex, but the southern margin of the SASM is influenced by the southern limit of the meandering ITCZ. This could demarcate a northern and southern part of the Amazon Basin within which secondary factors (e.g., location at the confluency of major rivers, eastern slopes of the Andes Mountains, deep river valleys, gallery environments) would be necessary to sustain moist forests during dry climatic cycles, and a central part where they would not be as necessary (see Chapter 8, Refugia).

Higher elevations are frequently drier because the ascending air is cool (less water-holding capacity) and has been depleted of moisture in the lowlands and the mid-altitudes. This contributes to the dry aspect of the Monte and the Gran Chaco of

Argentina and adjacent regions. Topography also affects rainfall by blocking the flow of moist ocean air to the leeward side of mountains and continental interiors (orographic deflection). Moisture from the westerlies is prevented from penetrating eastward by the Andes Mountains, further contributing to the dryness of the Monte and Gran Chaco. The upper elevations along the eastern side of the Guayana and Brazilian Highlands receive more rainfall than the western slopes, and the drier Pacific side of Panama results in part from partial blockage or redirection of moist air by the Cordillera Central. Mooretown on the windward north side of the Blue Mountains of Jamaica gets 5692 mm of annual rainfall, while coastal Kingston on the leeward side gets only 787 mm. Clearly, as topography changed during the Late Cretaceous and Cenozoic, this constituted a major forcing mechanism for climatic fluctuations and biotic response.

There is a myriad of other factors that determine climate, and each one interacts with the others to produce a system of positive and negative feedbacks. Volcanism initially cools global MAT by ~0.5° C for two to three years following a major eruption, such as occurred at El Chichón in Chiapas, Mexico, in 1982, through the absorption and deflection of heat energy by ash particles and droplets of sulphuric acid. Volcanism eventually warms global MAT by contributing CO_2 to the atmosphere creating a greenhouse effect (I: pp. 41–44). In turn, the rate of outgassing of greenhouse gases, such as methane, and CO_2 from mid-ocean ridges and terrestrial volcanoes bordering subduction zones is a function of plate movement. When plates are moving slowly, as at the current average rate of 2–3 cm/yr, CO_2 input into the atmosphere is less than when plate movement is faster. For example, subduction of the old Farallon (Pacific) Plate beneath the North American Plate during the Late Cretaceous and Paleogene is estimated at 12 cm/yr, and during the initial breakup of Pangea (or Pangaea) in the Jurassic it was 18–20 cm/yr. Atmospheric CO_2 concentration was high, temperatures were warm, glaciers were few, sea levels were high, continentality was reduced, temperature fluctuations were muted, equator-to-pole temperature gradients were low, and tropical and subtropical vegetation was widespread. In contrast, erosion of carbonate and silicate rocks during periods of intense mountain and plateau uplift causes a drawdown of CO_2 and lowers temperature (I: ch. 5; Pagani et al., 2005).

One way of envisioning the mechanism for change in net atmospheric CO_2 concentration over time is as a balance between pumps and sinks. Outgassing, melting of permafrost, and burning of the rain forest constitute pumps, while erosion of silicate rocks and storage of carbon in the complex molecules of plant and animal biomass constitute sinks. The ocean is the largest sink because large amounts of carbon are used in the formation of carbonate rocks (e.g., limestone) and stored in the form of carbonate ions in the shells of marine organisms (Feely et al., 2004; Sabine et al., 2004). Among vegetation types constituting prominent sinks are the vast expanses of tundra, peatlands (Smith et al., 2004), boreal forest (Schiermeier, 2005), deep-rooted grasses of the tropical savannas (Fisher et al., 1994), and the tropical rain forest. For example, the rain forest of Brazil is a net absorber of CO_2 at the rate of 8.5 ± 2.0 mol/m^2/yr (Grace et al., 1995; but see Saleska et al., 2003). Clearly, any biological or geological event that influences the absorption or release of CO_2 into the atmosphere will alter climate via changes in temperature. In turn, temperature affects global rainfall potential because more moisture is evaporated into the atmosphere from the ocean surface during warm intervals.

One such biological event is the removal of extensive tracks of vegetation, or the replacement of dense vegetation types (e.g., rain forest) by open ones (cerrado, desert, agricultural and pasture lands), through geologic processes or human activity. This not only affects global rainfall via transpiration (Kleidon & Heimann, 1999), but serves as a feedback to climate change through erosion and by altering albedo (reflectivity, as does the waxing and waning of ice sheets). Much of the natural semi-evergreen to deciduous forest of Guanacaste Province in northwestern Costa Rica is being cleared at the rate of ~3.0%/yr for farming, grazing, and construction of the Inter-American Highway. Not all of the life zones suffer equally, and most clearing, between 1961 and 1976, was in the more accessible lowlands: tropical moist forest, 7.6%; montane rain forest, 5.3%; premontane moist forest, 5.2%; tropical dry forest, 4%; premontane wet forest, 3.7%; tropical wet forest, 2%; lower montane wet forest 0.5%. Fleming (1986) hypothesizes that the observable trend toward lower rainfall in the region is due in part to clearing of the lowland forest. Also in Costa Rica, Lawton et al. (2001) have found that removal of the lowland forest results in fewer cumulus clouds, the cloud base becomes higher and, therefore, upwinds have less moisture to convey to the montane cloud forest.

Although the current destruction of biota and natural habitats, with concomitant modification of climate and reduction in the diversity of the gene pool, is widely recognized, land clearing has been going on for a long time in Latin America. For example, destruction of the natural biota on Barbados began in the early 17th century, and virtually all the natural vegetation had been cleared by 1665 to grow sugar cane. In contrast, forest cover in Puerto Rico has increased from less than 10% in the 1940s to 40% at present due to the shift from agriculture to manufacturing (Grau et al., 2003). Vegetation types changed markedly throughout the Late Cretaceous and Cenozoic, and evidence from modern analogs suggests the changes had a feedback to climate via gas exchange with the atmosphere (e.g., CO_2; Meir et al., 2006), MAP, and albedo.

Plate tectonics is an important factor in the history of vegetation and environments through its direct influence on mountain building (topography, rates of erosion), the movement of terranes, and, together with sea level changes, the opening and closing of land bridges (I: pp. 44–56). These events, in turn, play a role in determining atmospheric and ocean circulation, and all interact in a system of geologic events and biotic response. For example, the separation of South America from Antarctica ~30 Ma (a tectonic event) contributed to the ther-

mal isolation of Antarctica from warmer equatorial waters by allowing the development of a circum-Antarctic current that furthered the development of glaciers on the continent. Meltwaters from these glaciers formed part of the cold Humboldt Current that, together with the westerlies, dries the coast of Chile (a climatic change) producing desert vegetation (a biotic response).

Another example of tectonic cause and climatic–biotic effect involves the position and configuration of the South American continent. When South America was closer to Africa in the Paleogene, the bulge of northeastern Brazil deflected part of the equatorial Agulhas Current eastward toward Spain and the strength of the Gulf Stream was relatively weak. As South America moved westward, progressively more of the Agulhas Current flowed northward, augmenting the warm Gulf Stream now veering eastward farther north toward the British Isles, and intensifying thermohaline circulation in the Atlantic Ocean (I: fig. 2.6, pp. 34–35). Beginning in the late Eocene, sills began to form across the sea floor near the Isthmus of Panama, diverting more water into the Gulf Stream. The process continued until full closure of the isthmus at ~3.5 Ma, when present flow rates were attained. In addition to such changes induced by processes on Earth, there are long-term determinants of climate resulting from changes in the position of the Earth relative to the sun (Milankovitch variations), and possibly from fluctuations in solar luminosity (I: pp. 35–40).

The distribution of organisms and the composition of communities are determined by a complex of interrelated factors traditionally categorized as climatic, edaphic (soil), and biotic (pollinators, propagule dispersal potential, mycorrhizal associations, pathogens). Climate exerts a broad regional effect while edaphic and biotic factors refine the patterns of composition and distribution at more local levels. Therefore, a knowledge of present-day events and processes that determine climate and set climatic extremes is fundamental to understanding the present biota. A corollary is that an understanding of past events and processes that cause climates to change and the pattern of these changes is fundamental to understanding the history of biotas and how they developed through time. These factors are discussed further in (I: ch. 2), and in standard texts on climatology (e.g., Trewartha & Horn, 1980) and paleoclimatology (Crowley & North, 1996). The essential point is that the origin, development, and present status of the Earth's biota, both at the level of individual lineages and of ecosystems, cannot be fully understood by theorizing exclusively from modern assemblages, nor can it be understood simply by describing the composition of fossil floras and faunas from selected points in time. Ecosystems must be envisioned as dynamic continuums, with attention devoted to the causes for the dynamism,

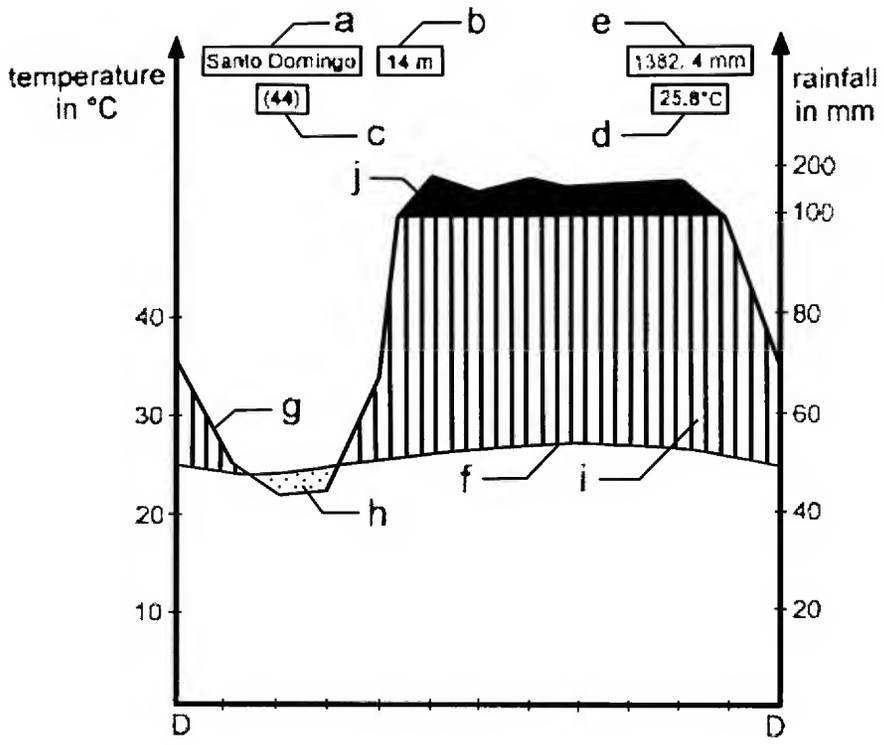


Figure 1.3. Climatogram used to summarize information on climate for specific locations (usually cities). The example used here is for Santo Domingo, Dominican Republic: *x* axis, Northern Hemisphere from January to December; *y* axis, one division corresponds to 10° C or 20 mm rainfall; a = meterological station; b = height above sea level; c = number of years of observation; d = mean annual temperature in degrees centigrade; e = mean annual precipitation in millimeters; f = curve of mean monthly temperature (1 division = 10° C); g = curve of mean monthly precipitation (1 division of 10° C = 20 mm); h = period of relative drought (dotted) for the climate region concerned; i = relatively humid season (vertical shading); j = mean monthly precipitation over 100 mm (scale reduced to 1/10, black areas are humid seasons). From Bolay (1997). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

and these causes derive in large part from interactions between geologic and climatic events and the Earth's bioclimate envelope (Pearson & Dawson, 2003).

Sources of information on the present climates of Latin America, in printed form, are the U.S. Department of Commerce/NOAA/National Climatic Data Center (1991), Martyn (1992), Bryson and Hare (1974), and Schwerdtfeger (1976). An electronic source is the World Climate Web site (http://www.worldclimate.com). Some additional information for selected sites in Latin America is provided in Table 1.2, and some regional and local sources are cited in the text. Conversion between metric and English equivalents can be made at several Web sites, including http://www.sciencemadesimple.net/conversions.html and http://www.onlineconversion.com. A convenient way of summarizing climatic data is through the Walter climatograms (Gaussen, 1955; Walter & Lieth, 1960–1967). An example with explanations is shown in Fig. 1.3, and others are included throughout the text.

Table 1.2. Representative climatic data for selected sites in Latin America. SL = sea level.

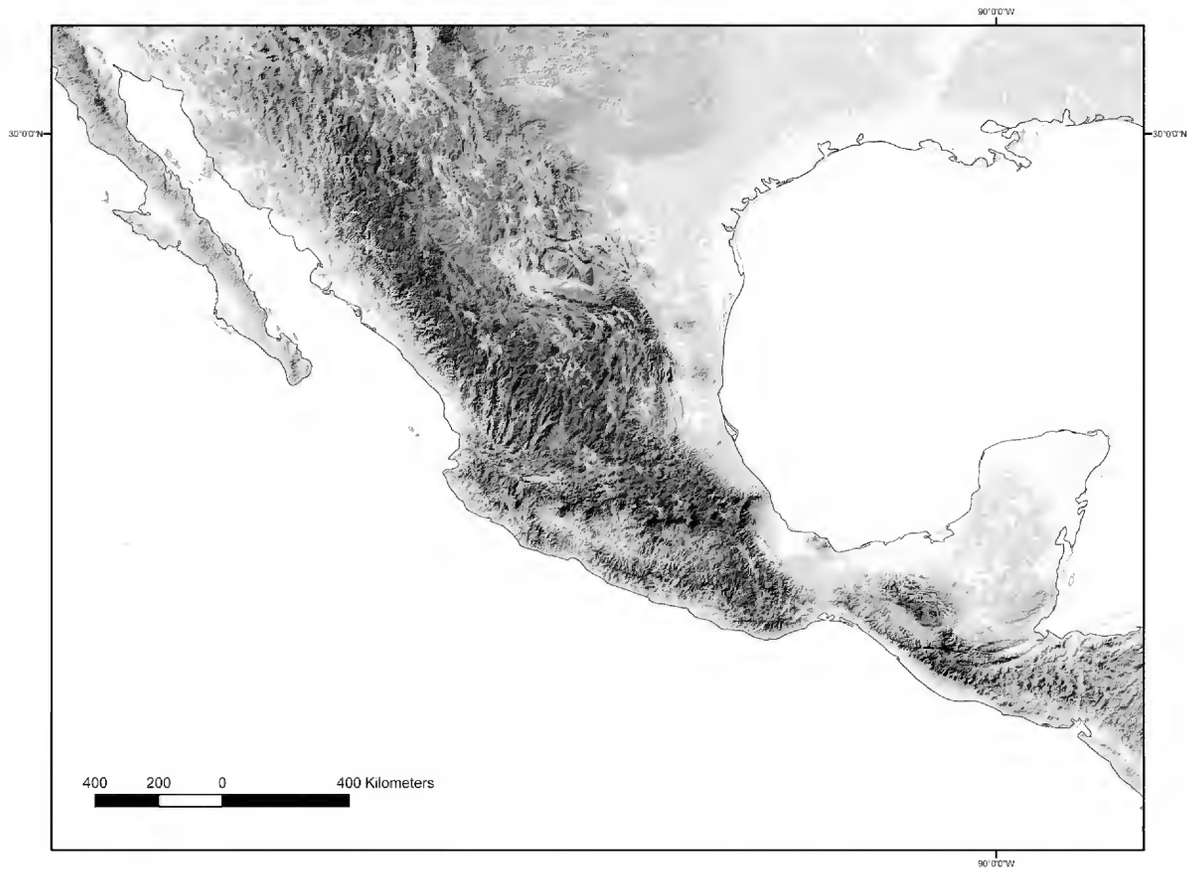
City, State	Elev. ft	MAT °F	Hot Mo	Cold Mo	MAP in/yr	Wet Mo	Dry Mo
Mexico							
La Paz, BCS	59	76	Aug 86	Jan 65	7.05	Sept 0.12	May 0
Guaymas, Son	13	77	July 88	Jan 64	9	Aug 2	May 0
Chihuahua, Chih	4669	–	–	–	15.7	July 3.9	Apr 0.1
Ciudad Lerdo, Dgo	3739	70	July 80	Jan 56	11	Sept 2	Mar 0.07
Monterrey, NL	1732	71.2	June 81.1	Dec 59.7	32.1	Sept 9.6	Feb 0.5
Tamaulipas, Tamps	239	76	Aug 83	Jan 67	40	Sept 11	Mar 0.5
Mazatlán, Sin	256	74.4	July 81.9	Jan 66.2	36.9	Sept 11.5	Mar 0
Zacatecas, Zac	8567	56	May 62	Jan 49	–	Aug 3	Mar 0.07
Guadalajara, Jal	5212	66	May 73	Jan 58	35	July 10	Mar 4
Guanajuato, Gto	6681	64	May 71	Jan 58	26	July 5	Feb 0.2
Pachuca, Hgo	7959	57.7	May 61.5	Jan 53.6	16.8	Sept 3	Dec 0.2
Morelia, Mich	6307	64	May 69	Jan 58	29	July 7	Feb 2
Mexico City, DF	7411	60	May 65	Jan 54	23	July 4.5	Jan 0.2
Toluca, Mex	8776	54.8	May 58.8	Jan 49.8	31.9	July 6.6	Feb 0.4
Cuernavaca, Mor	5062	68.6	May 73.8	Jan 65.3	40.9	Sept 10.1	Dec 0.1
Puebla, Pue	7053	61.3	May 65.8	Jan 55	31.7	Sept 7.4	Jan 0.3
Orizaba, Ver	4091	65	May 69.6	Jan 59.2	85.1	Sept 17.3	Mar 1.1
Veracruz, Ver	52	76.6	June 81.1	Jan 70.1	65.3	Sept 13.9	Mar 0.3
Acapulco, Gro	10	82	Aug 84	Feb 80	54	July 10	Mar 0.01
Salina Cruz, Oax	184	81	May 85	Jan 78	41	June 10	Apr 0.02
Huatusco, Ver	4000	60	May 70	Jan 58	69	July 11	Feb 0.2
Cozumel, Q Roo	10	78	June 81	Jan 73	61	Sept 9	Mar 2
The Antilles							
Cuba							
Nueva Gerona	197	77.7	July 81.9	Feb 71.8	70.6	June 11.1	Dec 1.5
Pinar del Río	77.7	–	July 82.8	Jan 71.8	63.4	Sept 10.5	Dec 1.2
Havana	79	77	July 82	Dec 72	47.7	June 6.6	Feb 1.9
Cienfuegos	98	76.3	Aug 80.6	Feb 71.2	38.7	June 5.9	Jan 0.7
Camajuaní	328	73.2	Aug 77.7	Jan 67.5	55.2	June 9.4	Feb 1.2
Camagüey	344	77.5	Aug 82	Jan 71.8	56.1	June 10.7	Jan 1.5
Santiago de Cuba	115	79	July 82	Jan 75	42.9	May 6	Feb 0.7
Jamaica							
S. Negril Point	32.8	78.4	July 80.4	Feb 75.7	55	Oct 7.9	Jan 1.9
Kingston	23	79	June 81	Jan 76	32.7	Oct 7	Feb 0.7
Morant Point	6.6	79.7	July 82.2	Feb 77.2	62.6	Oct 10.1	Mar 2.6
Hill Gardens	4921	62.2	July 65.1	Feb 59.2	93.2	Nov 19.7	July 2.7
Hispaniola							
Haiti							
Bayeux	36.1	76.6	July 80.2	Jan 72.3	81.7	Nov 15.4	July 1.8
Les Cayes	23	78.3	Aug 80.4	Feb 75.6	80.4	Oct 12.7	Dec 3
Ganthier	229.7	79.3	Aug 82.8	Jan 74.8	31.2	Oct 5.4	Jan 0.5
Port-au-Prince	123	79.9	July 83	Jan 77	51.7	Sept 6.9	Dec 1
Dominican Republic							
Pico Duarte	8890	–	Aug 62	Feb 58	–	–	–
Puerto Plata	39.4	77.9	Aug 82	Feb 74.5	65.5	Nov 13.4	July 3
Samaná	–	–	–	–	110	–	–
Sánchez	49.2	77.4	Aug 79.7	Jan 73.9	77.3	Nov 9.8	Feb 3.7
Santo Domingo	SL	–	81	75	–	–	–
Ciudad Trujillo	59.1	78	June 80	Jan 75	55.8	Sept 7.3	Feb 1.4
Puerto Rico							
Comerio Falls	492	76.6	Aug 79.2	Jan 73	79.2	Nov 8.9	June 4.8
Humacao	98.4	77.2	Aug 80.2	Jan 73.8	83.7	Sept 10.1	Mar 3.5
Mayagüez	78.7	77	Sept 79.5	Feb 74.1	80.9	July 11.5	Jan 1.9
Ponce	78.7	78.6	Aug 81.5	Jan 75.4	35.8	Oct 6.4	Dec 1.1
San Juan	98	78.2	Aug 80.8	Feb 74.8	62.8	Aug 7.1	Mar 2.3
Trinidad							
Port-of-Spain	25	80	May 81	Jan 78	54.5	July 7.8	Feb 1.2
Piarco	33	78.8	May 80	Jan 76.1	7.3	July 10.3	Feb 1.6
Tobago							
Crown Point	9	80	May 81.5	Jan 77.9	57.6	Oct 11.7	Feb 1.9
Central America							
Guatemala							
Quirigua	311.7	77.4	May 83.3	Nov 70.2	103	Aug 12.3	Apr 3.6
Salama	3018.4	72.7	May 77.5	Jan 67.8	30.1	June 9.2	Jan 0

Table 1.2. Representative climatic data for selected sites in Latin America. SL = sea level. *(Continued)*

City, State	Elev. ft	MAT °F	Hot Mo	Cold Mo	MAP in/yr	Wet Mo	Dry Mo
Guatemala City	4888.4	68	May 72	Jan 63	51.8	June 10.8	Feb 0.1
Quetzaltenango	7710	58.3	May 62.4	Jan 51.8	26.4	June 5	Dec 0.1
Belize							
Belize	SL	78	May 80	Dec 74	78.4	Oct 13.4	Mar 1.6
Augustine, Cayo	170.5	74.8	May 79.8	Jan 69.6	78.4	Oct 12.8	Apr 1.5
Honduras							
Tegucigalpa	3300	81.5	Mar 87.1	Nov 75.7	40.8	Sept 13.2	Feb 0.2
Choluteca	157	83.1	Apr 86.3	Sept 80.6	67.5	Sept 14.7	Jan 0.03
La Ceiba	185	80	May 84.9	Jan 75.7	118.4	Nov 19.9	May 3.1
Sta. Rosa Copan	1080	67.8	May 71.4	Dec 62.6	58.8	June 10.4	Mar 0.6
El Salvador							
Acajutla	49.2	80.7	Apr 82.9	Jan 78.9	67.2	Sept 14.9	Feb 0.03
San Salvador	2238	73.8	Apr 75.7	Nov 72.3	74.3	June 16.7	Mar 0.3
Nicaragua							
Puerto Cabezas	65.6	78.9	June 80.9	Jan 76.2	109.2	June 14.6	Mar 1.8
Bluefields	SL	79.5	Apr 82.4	Feb 77.7	127.7	Aug 23.5	Apr 1.1
Chinandega	209.9	80.2	Apr 83.6	Dec 78.6	75.1	Sept 19.0	Dec 0.3
Rivas	209.9	79.7	May 82	Dec 77.9	58.3	Sept 13.2	Mar 0.04
Costa Rica							
Puntarenas	9.8	80.4	Apr 83.1	Sept 78.9	66.2	Sept 13.6	Feb 0.05
San José	3723	67.5	May 68.9	Jan 66	75.9	Sept 14.2	Jan 0.2
Limón	9.8	77.3	May 78.9	Jan 75.2	138	July 20.4	Mar 6.2
Panama							
Bocas del Toro	6.5	78.9	May 80.6	Jan 77.3	128	July 16.6	Mar 5.7
David	86.4	80.2	Mar 82.5	Nov 78.8	99.1	Sept 16.9	Feb 0.9
Santiago	288.6	80.0	Apr 82.5	Dec 78.8	98.8	Oct 16.0	Mar 0.7
Cristóbal	36	81.2	Apr 82.4	Dec 80.6	128	Nov 21.1	Mar 1.5
Balboa	98	79	Mar 80	Aug 78	69.3	Oct 10.3	Mar 0.7
South America							
Venezuela, Aruba, Curacao							
Ciudad Bolívar	125	81.5	Oct 83	Jan 79.5	41.1	Aug 7.4	Feb 0.5
Caracas	2992	68.9	May 70.7	Jan 65.8	31.2	Oct 4.8	Feb 0.3
La Guaira	SL	80.8	Sept 82.9	Jan 78.4	11.1	Oct 4.8	Feb 0.3
Maracaibo	16.4	83.1	Aug 85.1	Jan 81.1	22.6	Sept 6.3	Feb 0
El Perú	721.8	77.5	May 79.2	Jan 75.6	55.8	June 8	Mar 2.1
Curacao	75.5	80.1	Sept 81.9	Jan 77.7	22.5	Nov 5.4	May 0.4
Mérida	5292	66.6	Sept 68.2	Jan 64.8	73.1	Oct 11.4	Feb 1.9
Colombia							
Bucaramanga	2999	73.8	Feb 74.6	Nov 72.6	44.6	Sept 6.3	Jan 1.6
Bogotá	8727	58.1	Mar 59	July 57.2	41.8	Oct 6.3	July 2.0
Medellín	4649	70.2	Jan 71.1	Oct 68.9	58.3	Oct 7.4	Jan 1.8
Andagoya	249.3	81.7	Apr 82.4	Nov 81	279.1	Apr 26.4	Mar 18
Barranquilla	SL	82.4	July 84.2	Feb 79.7	35.1	Oct 7.7	Jan 0
Ecuador							
Guayaquil	39.4	78.3	Apr 80.4	July 75.4	38.4	Feb 10.5	Aug 0
Quito	9248	55.7	Sept 56.1	Nov 55.2	46.2	Apr 6.5	July 0.7
Ambato	8595	57	Jan 58.5	July 54.5	17.9	Apr 2.1	June 0.7
Peru							
Arequipa	8041	56.8	Sept 57.9	July 55.6	41.7	Feb 1.81	June 0
Mollendo	80	80	Feb 70.7	Aug 59.4	0.85	Sept 0.19	Mar 0
Callao	SL	66.6	Mar 70.9	Aug 62.4	0.98	July 0.47	Mar 0
Lima	420	65.4	Feb 72.9	Aug 59.5	1.61	Aug 0.33	Feb 0.02
Cuzco	10,728	53.5	Nov 56.1	July 49.3	23.5	Jan 5.4	July 0.1
Trujillo	196.9	69.3	Jan 77.2	June 63	1.18	Feb 0.47	May 0
Iquitos	347.8	76.6	Nov 78.4	July 74.1	103.3	Dec 11.3	Aug 4.5
Bolivia							
Sucre	9350	54.3	Nov 58.1	July 49.5	26.2	Jan 6.2	June 0.1
Cochabamba	8448	63.1	Nov 68	June 57.2	18.2	Jan 4.1	June 0.2
La Paz	12,002	49.3	Nov 53.1	July 45.1	21.1	Jan 5.3	June 0.1
Chile							
Punta Arenas	92	44	Jan 52	July 35	19.2	May 2.2	Oct 1.0
Valdivia	19.7	52.9	Jan 61.9	June 45.5	105.4	June 17	Jan 2.4

Table 1.2. Representative climatic data for selected sites in Latin America. SL = sea level. *(Continued)*

City, State	Elev. ft	MAT °F	Hot Mo	Cold Mo	MAP in/yr	Wet Mo	Dry Mo
Puerto Montt	32.8	51.8	Jan 59.5	June 45.9	86.1	July 10.8	Feb 4.4
Valparaíso	135	59	Jan 64	June 54	19.8	June 5.7	Jan 0
Concepción	300	57	Jan 66	July 49	51	June 9.8	Jan 0.7
Santiago	706	57.4	Jan 69.1	July 46.0	13.1	June 3.1	Mar 0.1
Coquimbo	86.6	58.3	Jan 64	July 53.6	4.49	June 1.5	Jan 0
Antofagasta	308	63	Jan 69.6	July 57.2	0.16	June 0.04	Jan 0
Iquique	29.5	63.1	Jan 69.8	July 60.1	0.04	July 0.04	Jan 0
Tacna	1837.3	63	Feb 71.4	July 55.4	1.18	Jan 0.28	Feb 0
Guyana							
Georgetown	22	80.8	Oct 82.2	Jan 79.6	89.4	Nov 14.1	Sept 2.6
Suriname							
Paramaribo	12	81.5	Oct 83.8	Jan 79.7	87.3	June 11.7	Sept 3.1
French Guiana							
Cayenne	19.7	80.6	Sept 82.6	Jan 79.2	126.3	May 21.5	Sept 1
Brazil							
Belém	42	79	Apr 80	Aug 78	110.3	Mar 18	Oct 3.4
Manaus	133	79.9	Sept 81.9	Apr 78.3	82.8	Mar 12.5	Aug 1.8
São Luis	65.6	79.5	Oct 80.4	July 78.8	84.6	Mar 16.6	Oct 0.4
Natal	9.8	79.0	Jan 81	July 75.9	57.5	June 12.3	Nov 0.3
Ilhéus	147	75.5	Feb 78.8	July 71.1	83.1	Apr 12.5	Sept 3.9
Cuiabá	541	78	Oct 80.8	July 72.7	54	Jan 8.7	July 0.4
Corumbá	476	77.1	Dec 81.1	July 71.2	41.8	Dec 7.1	Aug 0.9
Goiás	1706	75.2	Sept 78.1	June 72.3	66.5	Jan 11.9	July 0.1
Belo Horizonte	2811	68.2	Feb 72.1	July 62.2	59.1	Jan 12.8	July 0.4
Petrópolis	2667	64.6	Feb 70	July 58.8	83.7	Nov 12.9	July 2.4
Rio de Janeiro	145	72.7	Feb 77.7	July 68.2	41	Mar 5.1	Aug 1.6
Santos	5	71.7	Feb 77.5	July 65.5	90.1	Mar 13.5	July 3.4
São Paulo	2612	64.4	Feb 69.6	July 58.8	53.3	Jan 8.5	July 1.0
Porto Alegre	49.2	66.9	Feb 76.5	June 56.3	49.8	Aug 5.1	Oct 3.1
Rio Grande	6.6	64.6	Feb 74.1	July 54.9	46.5	Feb 5.7	Apr 3
Uruguaiana	249.3	66.9	Jan 78.8	June 54.9	51.4	Mar 6.9	July 2.8
Salvador	28	76.6	Feb 79.3	July 73	72.3	May 11.9	Jan 3.4
Curitiba	2976	61.6	Jan 67.6	July 55.2	54.8	Jan 7.1	July 2.4
Paraguay							
Asunción	207	75.6	Jan 84.9	July 65.7	47.4	Mar 6.3	Aug 1.5
Argentina							
Corrientes	177	71.7	Jan 81.6	June 61.6	48.4	Mar 6.0	Aug 1.6
La Quiaca	11,358	48.4	Dec 54.7	June 37.4	11.3	Jan 3.2	May 0
Buenos Aires	83	62	Jan 74.5	July 51.3	40.1	Mar 5.5	Aug 2.5
Rosario	98.4	64	Jan 76.6	July 51.8	33.5	Nov 4.3	June 1.2
Santa Cruz	35	46.8	Jan 57.2	June 33.8	9.4	Apr 1.1	Oct 0.2
Bahía Blanca	82	59	Jan 71.8	July 47.1	19.6	Mar 3.6	Aug 0.7
Córdoba	1394	63.4	Jan 76.1	July 51.5	26.5	Dec 4.8	June 0.2
Tucumán	1466	67.1	Jan 77.6	July 55.3	37.8	Feb 6.9	July 0.3
Salta	3878	62.6	Dec 71.4	July 52.2	24.8	Jan 6.9	July 0
San Juan	2178	63.5	Jan 77.8	June 54.4	3.5	Jan 0.8	May 0
Mendoza	2477	59.6	Jan 74.3	June 45.1	6.0	Jan 0.9	June 0.1
Puerto Madryn	46	56.7	Feb 69.4	July 44.5	5.9	May 0.7	Aug 0.3
Uruguay							
Montevideo	96	61.4	Feb 73.2	July 50.4	42.4	June 5	July 2.4
Mercedes	128	62.8	Jan 75.4	June 50	34.3	Oct 3.9	Feb 2
Livramento	689	64	Jan 74.6	June 53.8	52.9	Mar 6.2	June 3.3



Baja California and Northwestern Mainland Mexico

The landforms of Mexico can be arranged into 12 major physiographic provinces (Figs. 1.4, 1.5; Table 1.3). Baja California is a peninsula ~1260 km in length and averages 95 km in width (85 km to 200 km). It is divided at the 28th parallel into Baja California Norte (capital Mexicali) and Baja California Sur (capital La Paz). There is a central mountainous region called the Peninsular Ranges with an average elevation of 1000 m consisting of the Sierra Juarez and the Sierra de San Pedro Mártir in the north (the latter includes the maximum elevation on the peninsula, La Providencia or Picacho del Diablo at 3078 m); the Sierra de la Giganta in the south; and smaller associated ranges and mountains. Although the central mountains are low in elevation, they still create a rain shadow on the eastern side. These are fault-block mountains with steep escarpments mostly facing the Gulf of California (Sea of Cortez, Sea of Cortés, or the Vermillion Sea). Off both coasts there are numerous islands (~110 along the east coast) representing submerged extensions of inland ranges (Wiggins, 1980, table 1, pp. 9–11). There is a narrow coastal plain on the east and a broader one on the west especially in Baja California Sur. The climate is dry, annual rainfall at places in the northeast is only 38 mm (1.6 in), temperatures there may reach 50° C (122° F), and much of the lowland peninsula is desert. Additional climate data are given in Table 1.2, and by García (1990), García and Mosiño (1968), and Hastings and Turner (1965). Baja California is separated from mainland Mexico by the 80–250 km wide Gulf of California. The waters of the Gulf are shallow and sudden storms can have devastating effects on small seacraft.[3] The Colorado River empties into the Gulf of California at its northern end and separates Baja California from Sonora on the mainland. This region is especially dry and one part, known as the Altar Desert, has moving sand dunes.

Six fossil floras are described from the area (four in Baja California Norte and two in Sonora; see Fig. 4.2). These include mega- and microfossil assemblages of Late Cretaceous (Campanian, 83.5 Ma) to Quaternary age pollen floras and rodent (packrat) middens. In addition there is some poorly preserved pollen of possibly Paleogene age in eroded sediments of the Gulf of California.

Altiplanicie (= High Plain; Central Plateau)

The northern and central part of middle Mexico is an elevated plateau consisting mostly of Mesozoic strata dissected by valleys, folded hills of mostly moderate elevation, and broad and shallow interior drainage basins or depressions (bolsones, cuencas), such as the Cuatro Ciénegas Basin in Coahuila and

Table 1.3. Political subdivisions of Mexico.

Federal District
States:

- Aguascalientes
- Baja California
- Baja California Sur
- Campeche
- Chiapas
- Chihuahua
- Coahuila
- Colima
- Durango
- Guanajuato
- Guerrero
- Hidalgo
- Jalisco
- México
- Michoacán
- Morelos
- Nayarit
- Nuevo León
- Oaxaca
- Puebla
- Querétaro
- Quintana Roo
- San Luis Potosí
- Sinaloa
- Sonora
- Tabasco
- Tamaulipas
- Tlaxcala
- Veracruz
- Yucatán
- Zacatecas

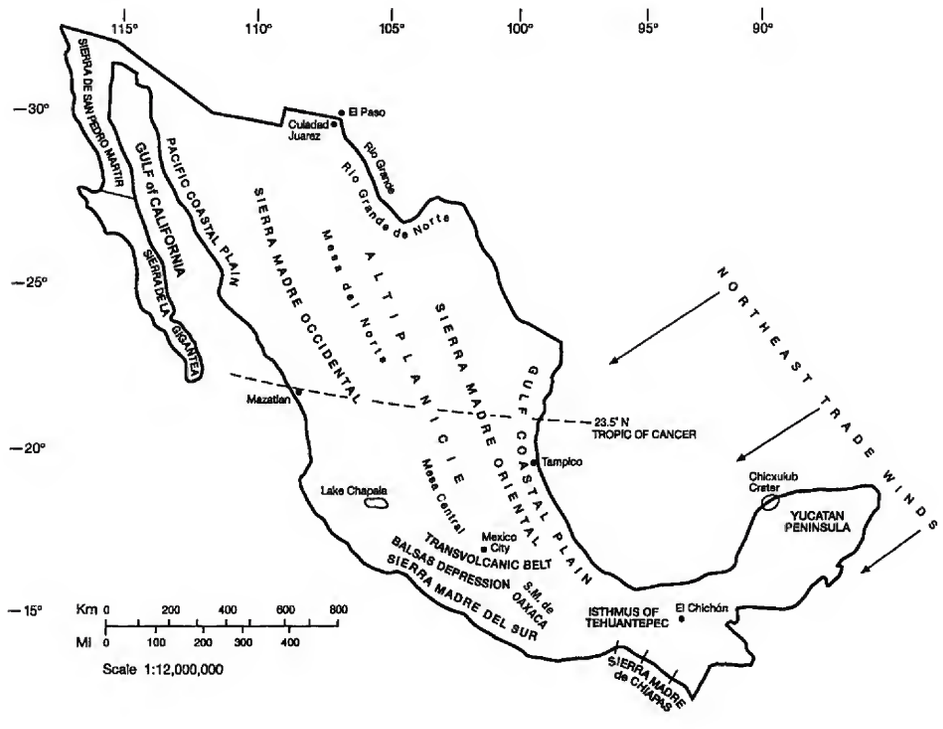


Figure 1.4. Physiographic regions of Mexico.

the Cuenca de Burgos in Nuevo Laredo. This is the Altiplanicie or Central Plateau (see Fig. 2.2). The average elevation is 915 m, and it is tilted upward toward the south, where elevations reach 2134 m, and slightly downward from the northwest corner (610–915 m) across the coastal plain to sea level in the northeast at Matamoras–Brownsville. The northern part from the United States border to about San Luis Potosí is the Mesa del Norte. Six megafossil and microfossil floras are known from the Central Plateau and the immediately adjacent Gulf Coastal Plain. Assemblages of Cretaceous (Maastrichtian) age are found in the Sabinas region of Coahuila, and plant microfossils have been recorded from deposits of the same age near Piedras Negras and from middle Eocene sediments of the Burgos Basin in Tamaulipas and Nuevo León in the vicinity of Nuevo Laredo. Other basins have accumulated Quaternary sediments containing spores, pollen, and diatoms, and packrat middens are found in rock shelters at several sites across northern Mexico. The latter are important sources of information on past vegetation from an environment where plant material is not readily preserved.

The Sierra Madre Occidental

These mountains border the western edge of the Central Plateau and are 1300 km long and up to 400 km wide (Fig. 1.6). They are composed of early Paleozoic crystalline igneous and metamorphic rocks overlain by lava and ash that was subsequently folded during the Tertiary into the rugged terrain of the present. The mountains are dissected by a number of valleys or barrancas including the scenic Barranca del Cobre or Copper Canyon in the state of Chihuahua.

The Sierra Madre Oriental

This mountain system borders the eastern edge of the Central Plateau and continues north as the Sacramento Mountains–Davis Mountains–Sierra Guadalupe of New Mexico, Texas, and northwestern Mexico. Near Emory Peak, Texas, at Big Bend National Park, these mountains block the Río Bravo del Norte (Río Grande) and create the characteristic right-angle bend in the river that separates Mexico from Texas between Ciudad Juárez and Matamoras. The Sierra Madre Oriental are composed mostly of folded sedimentary rocks of Jurassic and Cretaceous age that have eroded into structures mostly lower and more rounded than the crystalline and igneous rocks of the Sierra Madre Occidental. The maximum elevation is 3713 m at Cerro del Potosí south of Monterrey.

Transvolcanic Belt (Trans-Mexican Volcanic Belt, Eje Volcánico)

The southern margin of the Central Plateau terminates at a series of basins and mountains called the Transvolcanic Belt. Mexico City is located in one of these basins at an elevation of 2207 m on former Lake Texcoco. The water-saturated sediments preserve Quaternary spores and pollen, and cores have been taken from several of the basins. The removal of water, at a current rate of 60 m^3/sec, has caused significant problems of subsidence and water pollution for the ~20 million inhabitants of Mexico City (González-Morán et al., 1999). Cores required to test the foundation for construction (e.g., Torre Latinoamericana) and for engineering projects required to correct the tilt of some buildings, notably the Palacio de Bellas Artes, have provided additional material (for images of these and other structures see http://www.wcities.com). Plant mega- and microfossils occur in the Oligocene Pie de Vaca Formation to the southeast in southern Puebla.

The Transvolcanic Belt includes the highest peaks in Mexico—Pico de Orizaba (5650 m), Volcán Popocatépetl (5452 m, with glaciers on its northern face), Volcán Ixtaccíhuatl (5286 m; Fig. 1.7), Nevado de Toluca (4680 m), Colima (4339 m), Ajusco (3949 m), and Volcán San Martín Tuxtla (1550 m). The lapse rate in the mountains of central Mexico is 5.5° C/km (Lauer, 1973). It is a volcanically active zone, and volcanism is augmented by earthquakes that originate from subduction of the Pacific Plate beneath western Mexico along the Middle American Trench. Paricutín (Michoacán; 2773 m) emerged to great fanfare under the field of a Mexican farmer in 1943. Ejecta completely buried the villages of Paricutín and San Juan Parangaricutiro, leaving only the steeple of a church projecting above the ash and cinders. El Chichón, 650 km southeast of Mexico City, erupted in 1982; Mexico City was damaged by a severe earthquake in 1985; and Volcán Popocatépetl, 70 km northwest of Mexico City, began erupting on 30 June 1997 and more intensely during the week of 17 December 2000 after a 27-year dormancy. Video images of the December 2000 eruption can be seen on the Centro Nacional de Prevención de Desastres (CENAPRED) Web site at http://www.cenapred.unam.mx/mvolcan.html.

One of the largest rivers in Mexico is the Lerma River that flows from the Toluca Basin west of Mexico City into Lake Chapala (Fig. 1.8). The lake is a graben (down-faulted) basin, and it is the largest in the country. Lake Chapala and others in

the region, such as Lake Pátzcuaro, are the sites of Quaternary vegetation and environmental history studies for the Transvolcanic Belt region (see *Quaternary International*, Vols. 43/44, 1998). During past intervals of high rainfall (e.g., 28–25 Kyr), Lake Pátzcuaro probably drained into the Lerma River. The changes in precipitation and drainage patterns created geomorphic features such as saline layers and breached terraces useful in interpreting the plant fossil record.

Balsas Depression–Sierra Madre de Sur–Isthmus of Tehuantepec

Beyond the southern edge of the Transvolcanic Belt, the land drops sharply into the dry Balsas Depression (Fig. 1.9). The Balsas River has been dammed where it crosses the Sierra Madre de Sur in the state of Michoacán, and it is now a major source of hydroelectric power. South of the Balsas Depression are the mostly low mountains of the Sierra Madre de Sur (2438 m), and farther south is the mostly hot and windy lowland of the Isthmus of Tehuantepec. The lowland has an average elevation of less than 275 m and was one of four sites considered for the transoceanic canal. The others were across Nicaragua, the Darién region of eastern Panama and adjacent Colombia, and the eventual site across central Panama. The only information on the vegetation history are two Neogene megafossil floras from moister sites inland that have not been studied since the original publication in the 1920s, and Quaternary palynomorphs in a 1969 core drilled in the Middle American Trench off the Isthmus of Tehuantepec (9, 10, 23 in Fig. 4.2).

Figure 1.5. Political subdivisions of Mexico. A = Aguascalientes, BCN = Baja California Norte, BCS = Baja California Sur, C = Colima, COR = Cordoba, DF = Distrito Federal, GUA = Guanajuato, H = Hidalgo, M = Morelos, MC = Mexico City, Q = Querétaro, SLP = San Luis Potosí, T = Tlaxcala, TA = Tabasco, TG = Tuxtla Gutierrez, V = Villahermosa, ZAC = Zacatecas.

Figure 1.6. Sierra Madre Occidental looking west from near El Salto, Durango, Mexico. The pines are *Pinus ponderosa* and *P. montezumae*. Photograph by Jesse P. Perry Jr., used with permission of Jesse P. Perry III.

The Sierra Madre de Chiapas

These mountains are south of the Isthmus of Tehuantepec and continue into northeastern Guatemala as the Cordillera de los Cuchumatanes. They are one of five physiographic provinces in the state of Chiapas that also include the Pacific Coastal Plain, Central Depression, Front Ranges and High Plateaus (Chiapas Plateau, the Eastern Highlands, the Northern Highlands), and the Gulf Coastal Plain (Fig. 1.10; Müllerried, 1957). The state is topographically diverse and biologically one of the richest in Mexico. Elevations range from sea level along the Pacific coast, to 2900 m on the Chiapas Plateau, to 4220 m near Motozintla on the border with Guatemala. The region is drained by the Grijalva and Usumacinta rivers, flowing eastward into the lowlands of southern Veracruz and Tabasco, and the two rivers constitute one-third of the freshwater resources of Mexico. Climates are varied in Chiapas, with MAT ranging from 28° C on the Pacific coast to 12° C at the highest elevations. The MAP is 750 mm in the Central Depression to over 5000 mm on the lower Pacific slopes of the Sierra Madre de Chiapas (see also Table 1.2). In the vicinity of Simojovel and Ixtapa, sediments contain plant microfossils of late Eocene to Miocene age (Fig. 1.10; 7 in Fig. 4.2).

Yucatán Peninsula

The peninsula is part of a carbonate platform averaging ~200 m in elevation that continues south as the Petén region of Guatemala. It has a karst topography—a rough porous limestone without surface drainage and with numerous underground streams, caves, and sinkholes (cenotes; Perry et al., 1995). The cenotes preserve artifacts from the great ceremonial centers of the Maya such as Chichén Itzá and Palenque in Mexico and Tikal in Guatemala. The MAT ranges from 25° to 28° C, and MAP increases from the northwest (<500 mm) to

the southeast (1900 mm). Farther south on the peninsula in Belize and eastern Guatemala, MAP is 3000–4000 mm. Several palynological studies have been made on Quaternary deposits from the Yucatán area associated with lowland Maya archeological sites (e.g., at Cobá, 24 in Fig. 4.2).

Coastal Plains

Along much of Mexico, there is a coastal plain extending inland to ~200 m elevation. It is mostly narrow along the tectonically active Pacific Coast where the mountains are close to the ocean. Along the passive margin of the Gulf Coast it is 160 km wide in the north, narrows southward toward the eastern Isthmus of Tehuantepec, then broadens into the lagoons, estuaries, marshes, and mangrove swamps of the lowlands of southern Veracruz and Tabasco. Most of the sediments are derived from erosion of the Sierra Madre Oriental, and from as far away as the Rocky Mountains, transported by rivers such as the Río Bravo (Rio Grande). The northernmost extent of tropical rain forest in North America is in the lowlands of Veracruz, where the Universidad Nacional Autónoma de México (UNAM) maintains the biological station Los Tuxtlas near Catemaco.[4] The history of the vegetation and climate is preserved as fossil spores and pollen in the middle Pliocene Paraje Solo Formation along the Gulf Coastal Plain near Coatzacoalcos (12 in Fig. 4.2). The Yucatán Channel is a seaway only 210 km wide off the northern coast of the peninsula, and it separates Mexico from the Greater Antilles.

Figure 1.7. Ixtaccíhuatl Volcano, Puebla, Mexico. The pines are *Pinus hartwegii*. Photograph by Jesse P. Perry Jr., used with permission of Jesse P. Perry III.

Figure 1.8. Lake Chapala, Jalisco, Mexico.

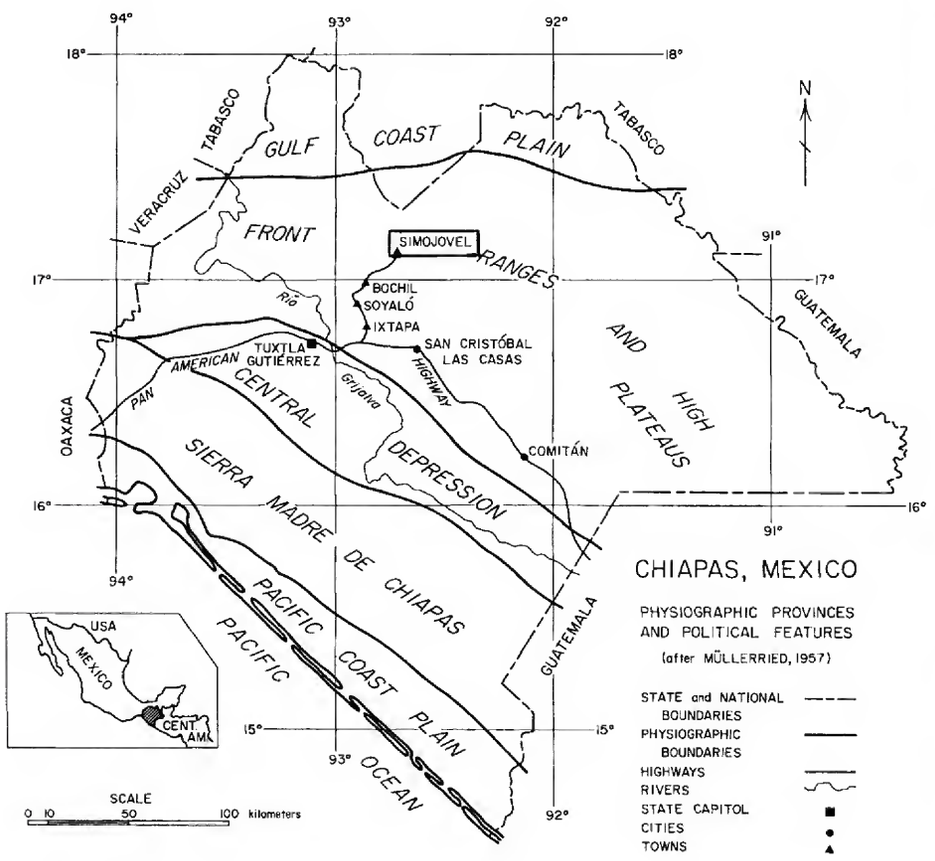
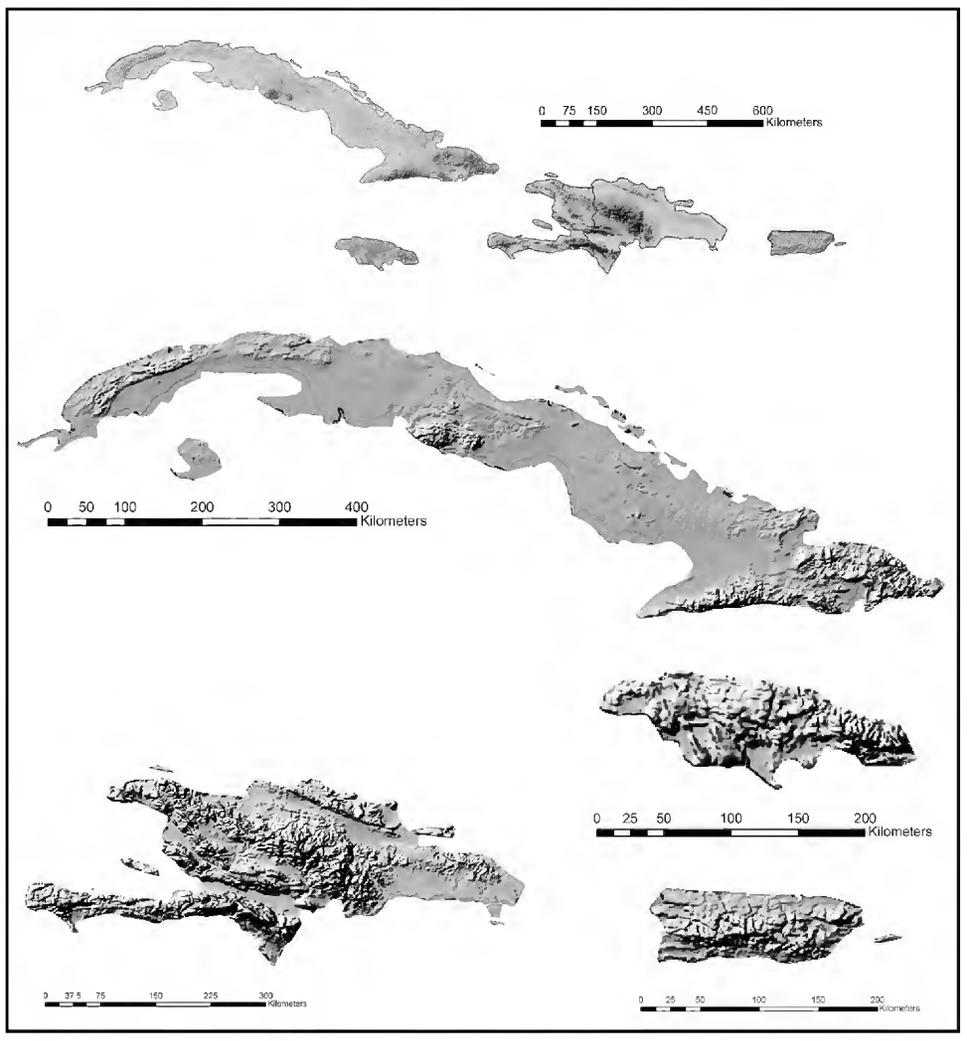


Figure 1.10. Physiographic divisions of the state of Chiapas, Mexico. From Frost and Langenheim (1974). Used with permission of Northern Illinois University Press, DeKalb, Illinois.

Figure 1.9. Balsas River, Michoacán, Mexico.

THE ANTILLES: The Islands of the Caribbean



"On October 5 [1492] the restless crew was encouraged by flocks of birds flying their way. Then, thirty-three days out, at two o'clock on the morning of October 12, a lookout on the *Pinta* claimed the announced 5000-maravedi bonus, for he was the first to shout 'tierra! tierra!'—the island of San Salvador." (Daniel J. Boorstin, *The Discoverers*)

The Greater Antilles

The Greater Antilles consist of the islands of Cuba, Jamaica, Hispaniola (Haiti and the Dominican Republic), Puerto Rico, the small easternmost U.S. and British Virgin Islands, and numerous small cays or keys (Fig. 1.11). These extend in an arc-like configuration from ~85°W longitude near the Yucatán Peninsula, to just south of Florida, eastward to ~60°W longitude. A collection of maps of the Antilles dating from 1511 to the early 1900s assembled by Blair Hedges is available at the Caribmap Web site (http://www.caribmap.net). Farther east and south are the Lesser Antilles, and to the north are the 300 islands of the Bahamas. The Antilles are situated around the margin of the Caribbean Sea, which has a surface area of 2,754,000 km^2 and is slightly larger than the Mediterranean Sea at 2,505,000 km^2. The distances between the islands are not great—Cuba is separated from Florida by the Florida Straits (160 km wide and ~700 m deep), from Yucatán by the Yucatán Channel (210 km wide and 2000 m deep), and from Haiti by the Windward Passage (72 km wide and 4000 m deep). The Dominican Republic is separated from Puerto Rico by the Mona Passage (96 km wide but with the intervening Mona Islands), and from Jamaica by 140 km; Haiti from Jamaica by the Jamaica Passage (180 km wide and 3000 m deep); the Virgin Islands from the Lesser Antilles island of Anguilla by the Anegada Passage (112 km); and Tobago from Trinidad (34 km). The greatest depths are 9220 m in the Puerto Rican Trench along the northern margin of the Greater Antilles (deepest in the Atlantic Ocean), and 6800 m in the Cayman Trough extending northeast from the junction of Guatemala and Honduras (Ladd et al., 1990, p. 262). These may be compared with the greatest depths in the Gulf of Mexico at 5203 m, the Mediterranean Sea at 5121 m, and the greatest of all ocean depths along the Mariana Trench east of the Philippine Islands at 11,022 m.[6] The highest elevation in the Greater Antilles is Pico Duarte (Mount Trujillo) at 3098 m in the Dominican Republic (Orvis, 2003). The next highest is the adjacent Loma La Pelona at 3094 m. In considering the historical biogeography of the Caribbean (e.g., the likelihood for dispersal), it is worth noting that the islands are close, they have been so throughout their history, and various components have been emergent for 45 million years.

The islands lie along the route of the northeast trade winds and, thus, along the path of hurricanes that come mostly from the southeast. These are a characteristic albeit irregular feature of the Caribbean environment and are being increasingly recognized as important in Caribbean forest dynamics by creating canopy gaps (Fig. 1.12; Osborne, 2000, gap theory, pp. 264–266).

Throughout the Antilles, generally there is a bimodal distribution of rainfall in May–June and in September–November

broadly associated with the twice-yearly passage of the sun directly overhead at the equinoxes. The wet months typically receive 500–600 mm of rainfall, while in the driest months it may be less than 25 mm. Annual temperatures average 25°–28° C at 2400 m, and 22°–25° C during the coldest months of January and February. Additional climate data for representative sites in the Antilles are given in Table 1.2. There are no active volcanoes in the Greater Antilles and major earthquakes are relatively rare, although there are tremors from subduction along the Puerto Rican Trench. A large earthquake devastated Port Royal, Jamaica, in 1692, and another occurred in eastern Cuba in 1942. The most intense volcanic activity is in the Lesser Antilles. Fourteen fossil floras are known from the Greater Antilles (Fig. 5.1). The oldest is Cretaceous, but the age within that period is unknown, and the youngest are spore and pollen assemblages from the Holocene of Cuba and the Dominican Republic.

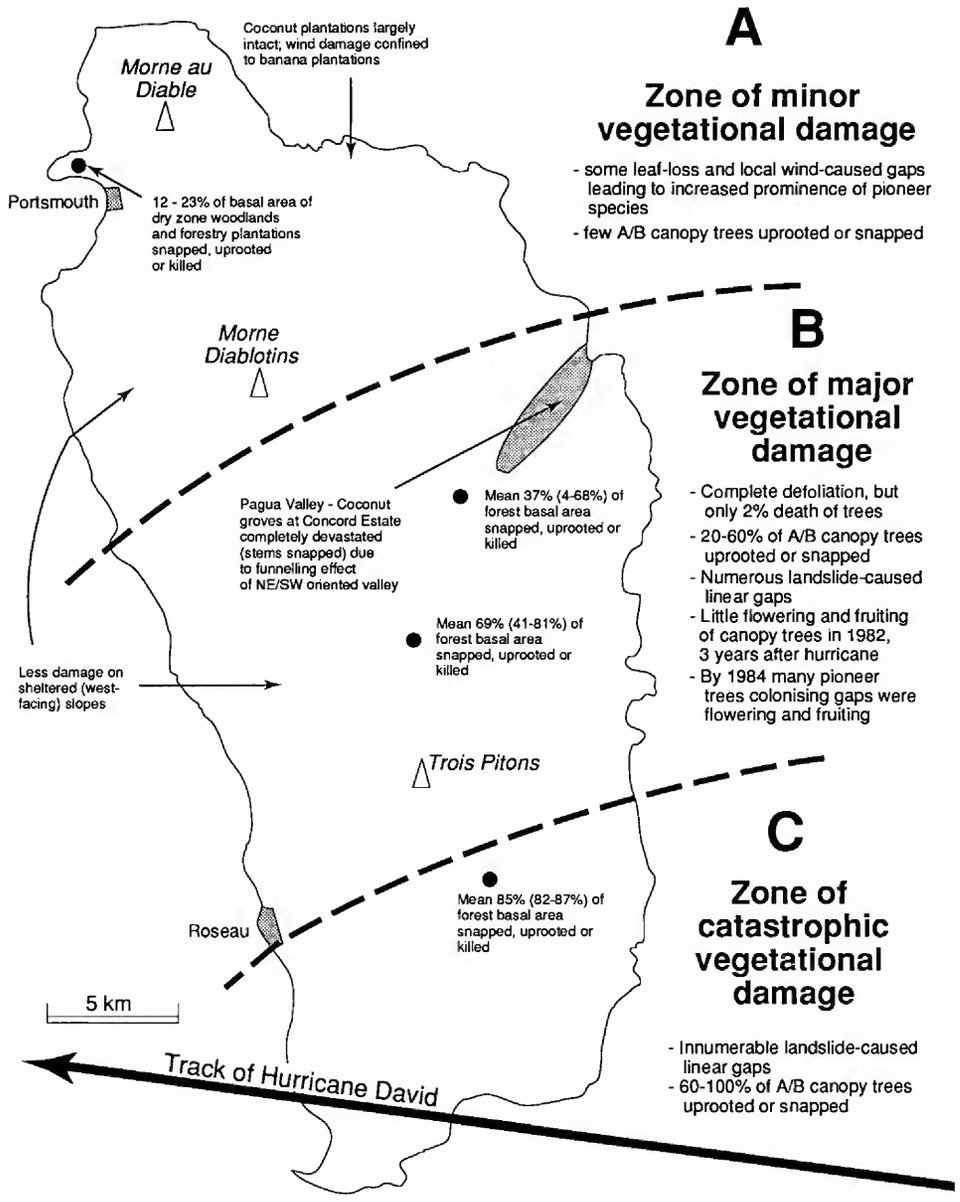


Figure 1.12. Zonal damage of vegetation on Dominica from Hurricane David, August 1979. From Walsh (1996). Reprinted with the permission of Cambridge University Press.

Cuba

> "Cuba has the same effect on Americans that the full moon used to have on werewolves." (Alan Ryan, ed., 2000, *The Reader's Companion to Cuba*, Harcourt & Brace, New York; see also the documentaries *Fidel*, a film by director Estela Bravo, and *Cuba: Wild Island of the Caribbean*, Nature Videos)

Cuba is the largest island of the Antilles. The Isle of Pines, named the Isla de la Juventud (Isle of Youth) in 1976, is located to the south 96 km across the Gulf of Batabano. Prior to 1976, the provinces of Villa Clara, Cienfuegos, Sancti Spíritus, and Ciego de Ávila were part of Las Villas Province, and the land east of Camagüey was part of Oriente Province. The relationship between the new and old province names is shown in Fig. 1.13 and Table 1.4. There are also ~4200 small mangrove-fringed cays in the adjacent shallow waters, giving the Cuban Archipelago a combined area of ~110,922 km^2. The principal mountains are the Sierra Maestra in the southeast with Pico Turquino (Real), west of the United States naval base at Guantánamo, the highest in Cuba at 1974 m. The Sierra del Cristal to the northeast reaches elevations of 1231 m. Other mountains are the western Sierra Guaniguanico in Pinar del Río Province, which includes the Sierra de las Organos and the Sierra del Rosario with El Pan de Guajaibón at 692 m. The Sierra del Rosario region is noted for its distinctive limestone mogotes—mesas that rise 300 m above the surrounding rolling plains (Fig. 1.14). The Sierra de Trinidad is on the south coast of Sancti Spíritus Province, and the highest elevation there is San Juan Peak at 1156 m. These combined highlands cover about one-fourth of Cuba and the remainder is mostly plains. The MAT is 23° C at Camajuaní in central Cuba near Santa Clara and 26° C at Santiago de Cuba on

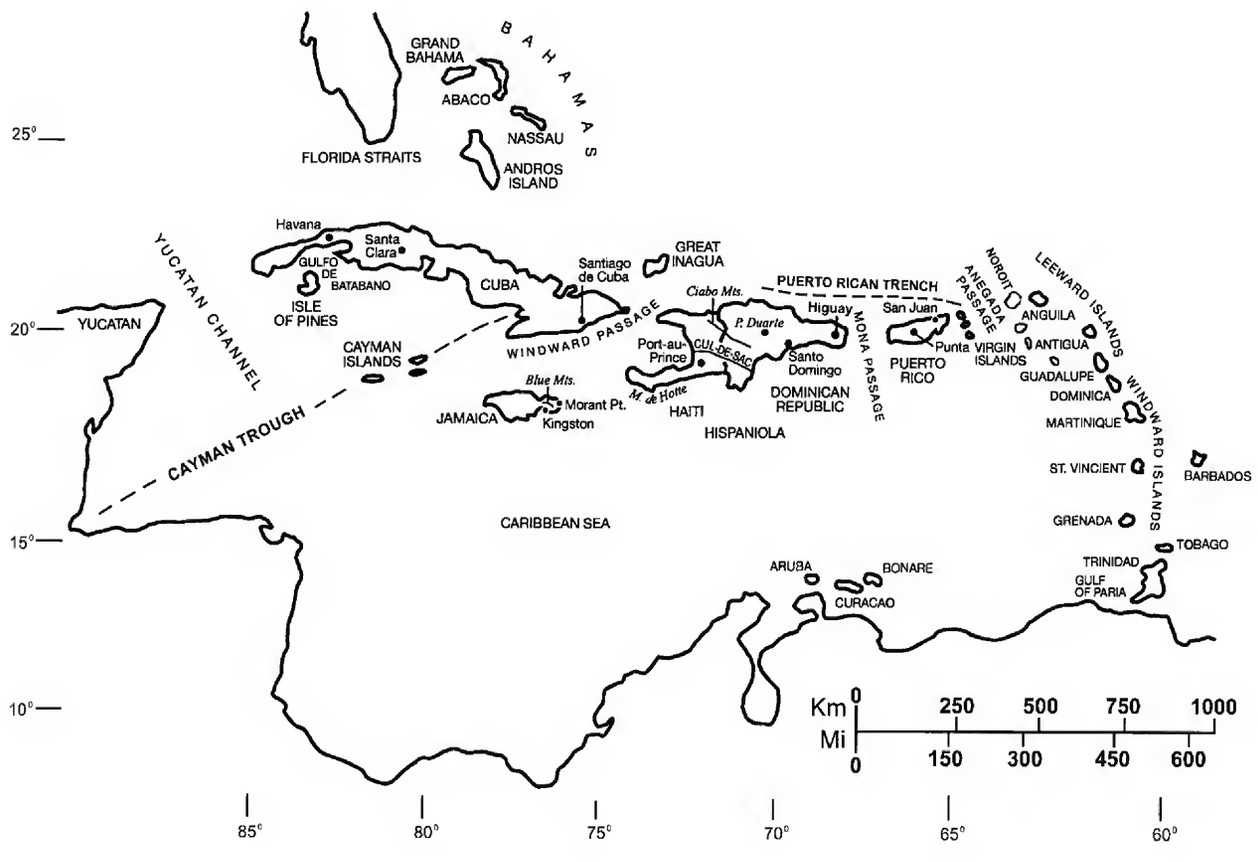


Figure 1.11. Islands of the Caribbean Basin.

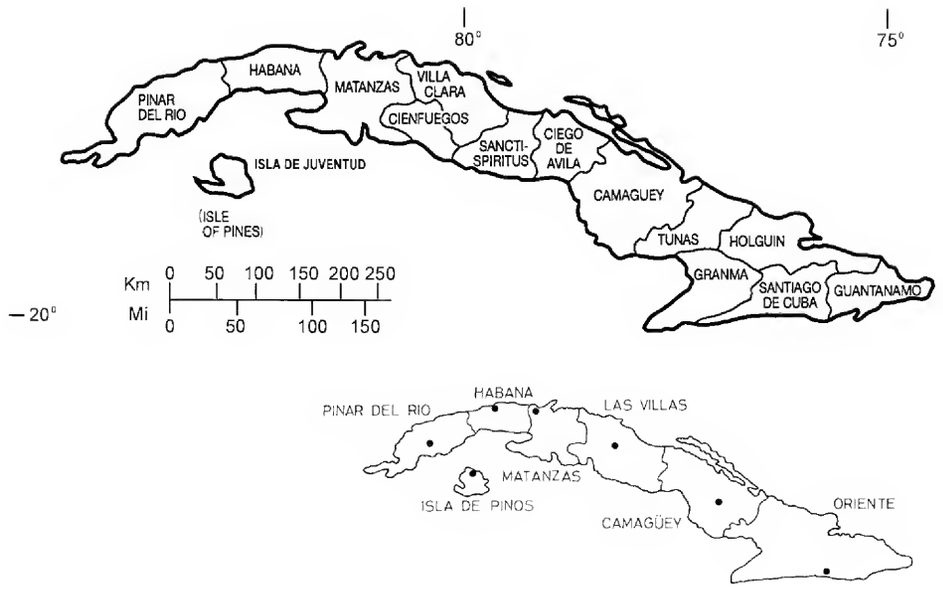


Figure 1.13. Political subdivisions of Cuba with pre-1976 subdivisions shown in smaller inset (latter from Borhidi, 1996, used with permission of Akadémiai Kiadó, Budapest).

the eastern end of the island (Fig. 1.15). Annual rainfall is 1090 mm at Santiago de Cuba and 1793 mm at Nueva Gerona on the Isla de la Juventud. Other climatic data are given in the *Atlas de Cuba* (1978) and in Table 1.2. Five fossil floras are recorded for Cuba, including plant megafossils from the Tertiary of Matanzas Province. Plant microfossils are known from the Cretaceous of Matanzas Province; the middle Eocene Saramaguacán Formation of Camagüey Province; and the Quaternary of eastern mainland Cuba and from off the western end of the Isla de la Juventud.

Jamaica

Jamaica is mountainous with nearly 90% of the island consisting of highlands surrounded by a narrow coastal plain. The western and central portion is a highly dissected karst or limestone plateau of ~30 km^2 called the Cockpit Country. The Blue Mountains constitute the eastern one-third of the island and have a maximum elevation of 2255 m at Blue Mountain Peak.

The MATs are 26.5° C at 2 m elevation at Morant Point, 16.7° C at Hill Gardens at an elevation of 1500 m, and 13.3° C near the maximum altitudes of the Blue Mountains for a lapse rate of 5.3° C/km. Annual precipitation on the northern windward side of the island is 5639 mm at Mooretown, 2367 mm at Hill Gardens, and 830 mm at Kingston on the southern leeward side. Plant microfossils are known from the middle Eocene Guys Hill Formation near Christiana in central Jamaica.

Haiti and the Dominican Republic (Hispaniola)

Haiti is about one-half the size of the Dominican Republic (27,750 km^2 versus 48,734 km^2), but with nearly the same population (6,625,000 versus 7,313,000; Table 1.1), it has double the population density, which is one reason for the virtually complete destruction of natural habitats and the severe environmental degradation. The physical geography of Haiti is similar to that of other Greater Antillean islands in that coastal areas rise to a central cordillera. A structural depression called

Table 1.4. Political subdivisions of Cuba.

City: La Habana; Provinces: Camagüey, Ciego de Ávila, Cienfuegos, Granma, Guantánamo, Holguín, La Habana, Las Tunas, Matanzas, Pinar del Río, Sancti Spíritus, Santiago de Cuba, Villa Clara; Special municipality: Isla de la Juventud.

the Cul-de-Sac/Enriquillo Basin extends from Port-au-Prince in Haiti to Neiba Bay in the Dominican Republic and represents the contact between two land fragments that collided in the late Miocene. The average elevation along the depression is only +40 m msl (mean sea level), points along the basin are even below sea level, and hurricanes crossing the Caribbean Sea are frequently funneled through these lowlands. On 7 December 2003, tropical storm Odette crossed Hispaniola, and is the first recorded storm to form this late in the Caribbean. [In contrast, Hurricane Adrian is the earliest recorded storm to cross Central America, 17 May 2005.] Haiti is on the leeward side of the northeast trade winds, and average rainfall is less than it is on the mostly windward Dominican Republic. Annual precipitation in Haiti is from a low of 500 mm in the west to more than 2000 mm in the uplands in the east. The northwestern peninsula and Gonâve Island are the driest. The warmest part of Haiti is in the west where MAT is 26.7° C, and it is cooler in the interior highlands as at Kenscoff (1432 m) where the MAT is 24.4° C. The Massif de la Hotte is a low mountain range in southwest Haiti, and the principal river is the Artibonite. Plant megafossils from the Mio–Pliocene Artibonite Group are found just north of the Cul-de-Sac/Enriquillo Basin, and fossil spores and pollen are known from the same site. Plant microfossils of Quaternary age occur in sediments of Lake Miragoane on the north side of the southern peninsula.

In the Dominican Republic, the principal mountain chains are the Cordillera Central or Cibao Mountains and the Cor-

Figure 1.14. Mogote, Sierra del Rosario region, Cuba. Photograph by David Bogler.

dillera Septentrional to the northeast, separated by the Cibao Valley and drained by the Río Yanque del Norte (Fig. 1.16). The average MAT for the Dominican Republic is ~25.5° C in the coastal lowlands, and it decreases with increasing elevation to 9°–10° C at Pico Duarte, for a lapse rate of 5° C (Constanza, 1200 m to Pico Duarte, 3098 m). Rainfall is highest in the uplands of the northeast at 2540 mm and lowest in the far northwest and southwest at 500 mm. A series of climate diagrams across the Dominican Republic from the south (Perdenales) to the north (Puerto Plata) is shown in Fig. 1.17. Plant megafossils of Cretaceous age occur just north of Santo Domingo, and others of Late Tertiary age are found in the District of Samaná on the north coast, but like all the megafossil floras of the Antilles, these have not been revised since the original publications in the early 1900s. The famed Dominican amber of Miocene age is mined from sites in the Cordillera Septentrional and contains inclusions of bacteria, fungi, bryophytes, ferns, angiosperms (e.g., orchids), and a varied fauna (including bees). Quaternary sediments from the center of the Dominican Republic extending back to ~11.4 Kyr B.P. contain spores, pollen, and charcoal that reflect hurricane disturbance and fire history (lightning) prior to the arrival of humans about 7000 years ago, and the beginnings of agriculture about 2000 years ago.

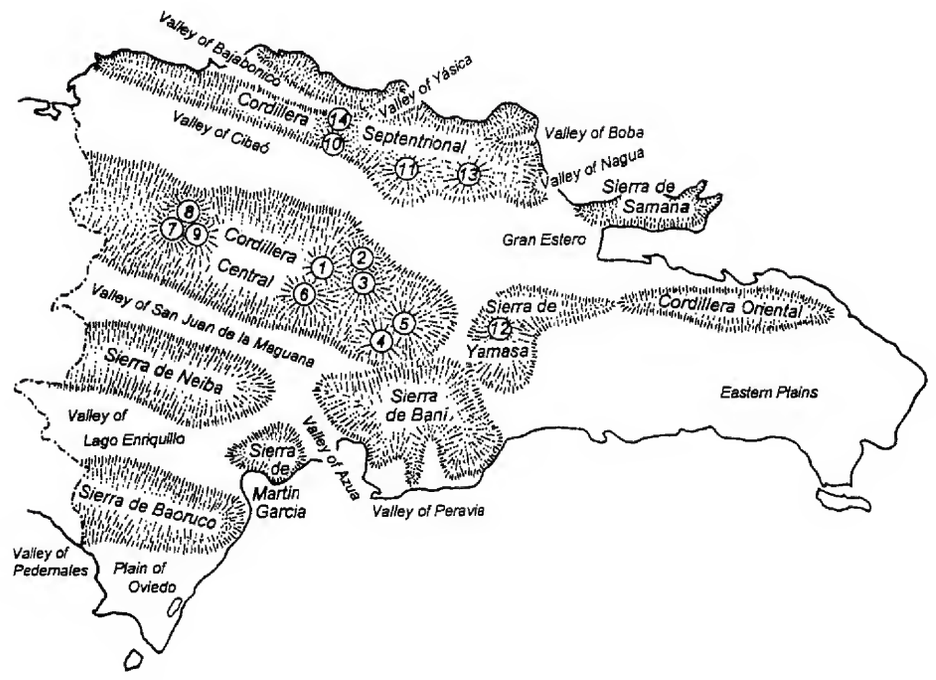


Figure 1.16. Mountain ranges and basins of the Dominican Republic. Numbers refer to the highest peaks in the Dominican Republic: 1 = Pico Duarte, 2 = La Pelona, 3 = La Rucilla (3049 m)/Pico Yaque (2760 m), 4 = Monte Tina, 5 = Monte de Alto, 6 = Monte Mijo, 7 = Monte Nalga de Maco, 8 = Monte Gallo, 9 = Jicomé, 10 = Diego de Ocampo, 11 = El Peñon, 12 = El Mogote, 13 = Quita Espuela, 14 = Isabela de Torres. From Bolay (1997). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

Puerto Rico

Puerto Rico includes the main island and the three offshore islands of Mona to the west and Vieques and Culebra to the east. The Cordillera Central divides the mainland into a wet northern side and a drier southern side. The peak of El Yunque (the Anvil) on the north receives 4572 mm of annual rainfall, while Ponce on the south coast receives only 910 mm. The highest peaks are the Pico de Jayuya–Mont Punta at 1338 m in the center of the island and El Yunque at 1077 m in the northeast.

Representative MATs are 25.6° C in the coastal lowlands. They become progressively lower in the uplands—22° C at Cayes at 411 m and 20° C at Torro Negro Dam at 693 m. Annual rainfall along the northern coast averages ~2330 mm, while on the adjacent slopes it is ~4100 mm. Both plant mega- and microfossils occur in the middle Oligocene San Sebastián Formation in the central uplands of western Puerto Rico.

Virgin Islands

These small islands constitute the eastern terminus of the Greater Antilles. The topography of the U.S. Virgin Islands (St. John, St. Croix, St. Thomas) is low, and the climate is similar to that at low to middle elevations on the adjacent islands. Tortola is the main island of the British Virgin Islands, and it is similar in topography and climate. There are no fossil floras described for the Virgin Islands.

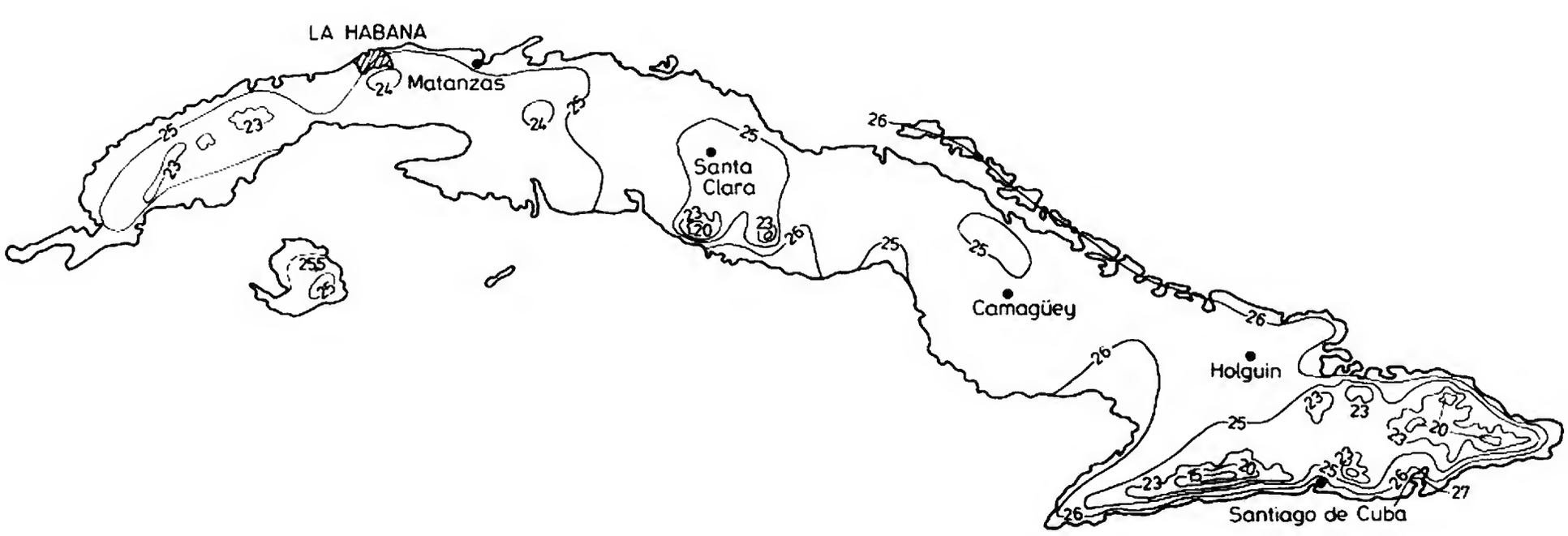


Figure 1.15. Mean annual temperature data for Cuba. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

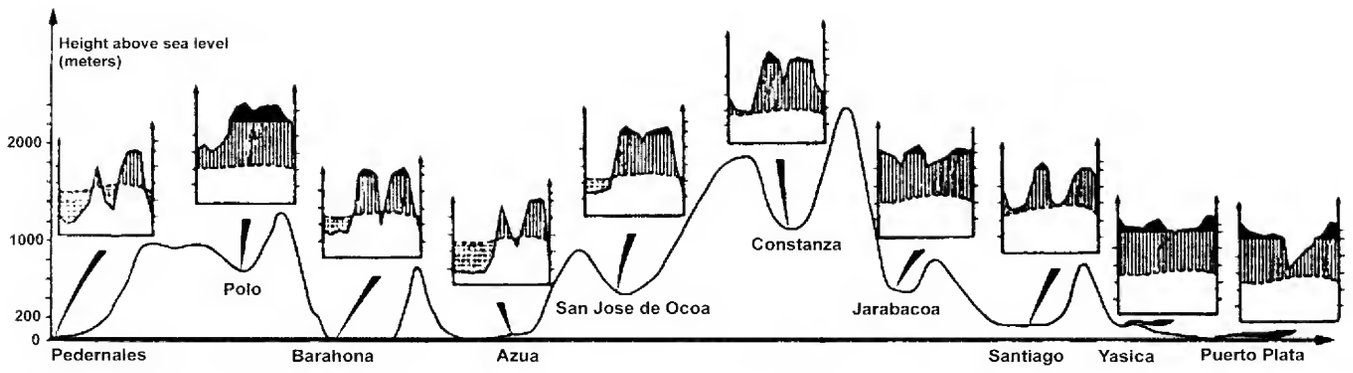


Figure 1.17. Climatograms along a transect from Pedernales (south) to Puerto Plata (north), Dominican Republic. From Bolay (1997). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

The Lesser Antilles

It is tempting to regard the Lesser Antilles of limited importance to the vegetation history of the Caribbean region because there are no fossil floras known from the islands. Nevertheless, their emergence in the middle Eocene played a role in modifying ocean circulation in the west-central Atlantic Ocean, and they facilitated migrations of plants and animals between South America and the Greater Antilles. The coral reefs of Barbados are also the site of Quaternary paleotemperature and sea-level studies that are important for comparing the marine paleoenvironments of the tropical western Atlantic with high-latitude temperate regions.

The Lesser Antilles (Fig. 1.18) are separated from the Greater Antilles by the Anegada Passage between Anguilla and the Virgin Islands (17°N latitude). They extend southward to Grenada, then westward along the northern coast of South America to Aruba, Bonaire, and Curaçao (12°N latitude). The strongest winds come mostly from the southeast, so the islands from Grenada to Guadeloupe, including Barbados 160 km farther east, are called the Windward Islands. Those extending from Anguilla to Antigua are the Leeward Islands.[7] The Lesser Antilles are either coral limestone islands (the Limestone Caribees) with only moderate relief, or volcanic islands providing spectacular scenic views (e.g., Martinique with its famed volcano Mt. Pelée). This volcano erupted on 8 May 1902, killing 30,000 people in St. Pierre and devastating five other towns on the island. There were only two survivors in St. Pierre, one of whom was a prisoner being held in a local jail for wounding a friend with a sword. He was known by several names including Louis-Auguste Cyparis and "Samson." Near the very end of his sentence he escaped, partied all night, and turned himself in the next morning. He was sentenced to solitary confinement and held in an underground cell used for that purpose. On 8 May, heat and fumes from the eruption burned him badly, but he survived and four days later he was released. For his ordeal he was pardoned, joined the Barnum & Bailey Circus and toured the world as "the lone survivor of Mt. Pelée" (Zebrowski, 2002). Mt. Soufrière on St. Vincent erupted in 1979, and the volcano on Montserrat erupted in August 1997.

Barbados is an eastern outlier of the Lesser Antilles separated by the Tobago Trough. It has a flat to rolling surface with a maximum elevation of only 335 m at Mt. Hillaby. Temperatures are uniform throughout the year, averaging 27° C in August and 25.5° C in February. Annual rainfall is 1525 mm, and the rainy season is between June and November.

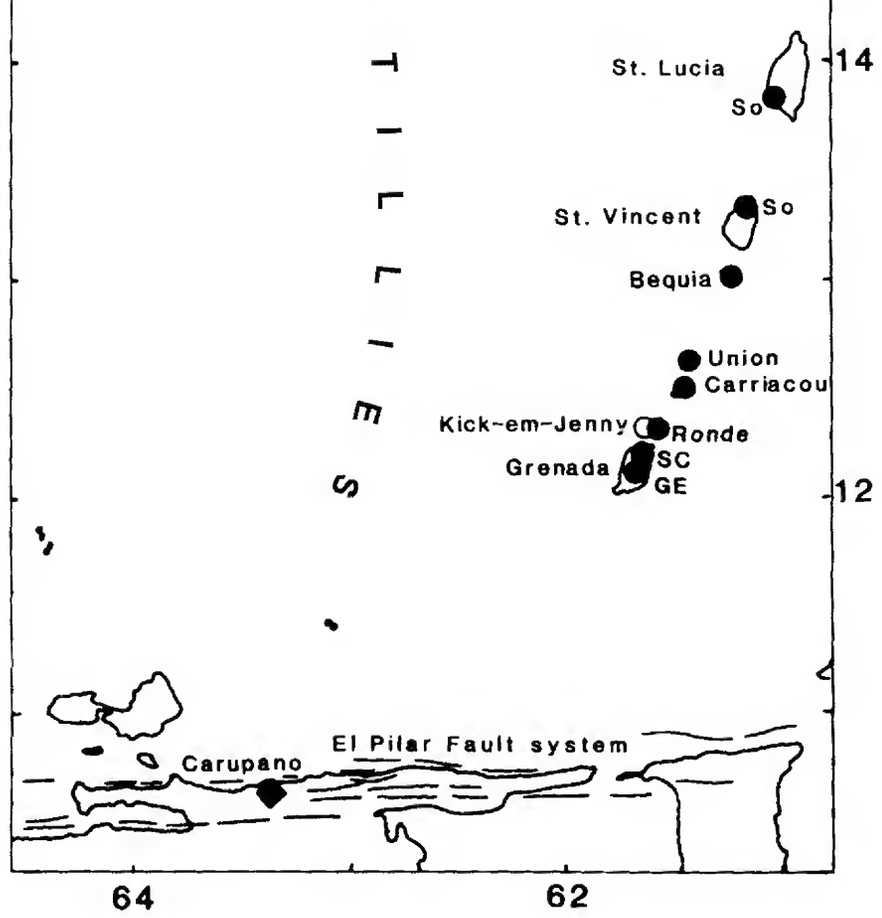
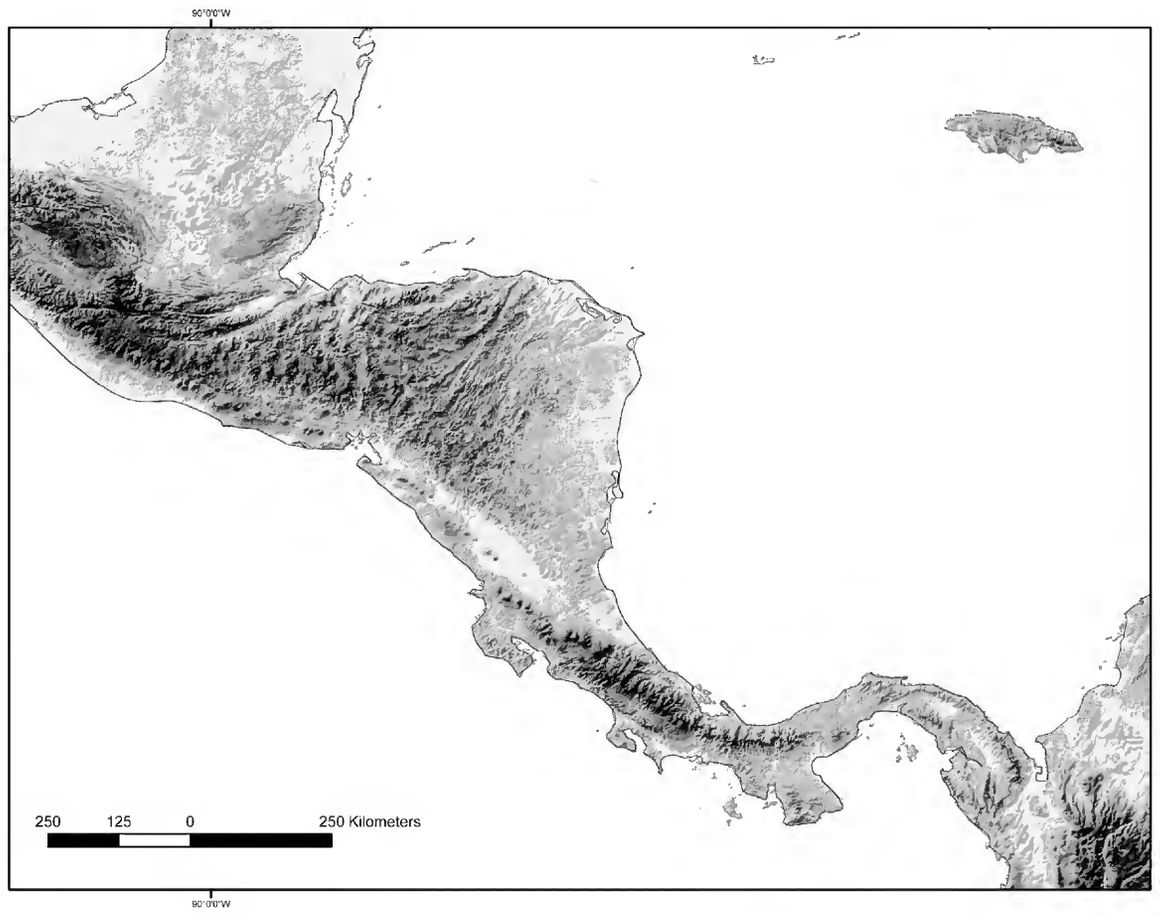


Figure 1.18. Active volcanic centers in the Lesser Antilles. Solid circles indicate emergent volcanoes. Open circles indicate submarine volcanoes. From Donnelly et al. (1990). Courtesy of Geological Society of America.

Trinidad and Tobago are geographically and geologically part of South America rather than the Antilles. Columbus encountered Trinidad on his third voyage in 1498 and named it in honor of the Holy Trinity, possibly suggested by the three low mountain ranges that rise to 915 m. Annual rainfall is from 1525 mm along the Gulf of Paria to 3810 mm in the mountains of Trinidad. Tobago is 34 km northeast of Trinidad and consists of 300 km^2 of mostly mountainous terrane. A few megafossil plants of Tertiary age are known from Trinidad, and there are reports of plant microfossils, mostly unpublished as part of oil and gas surveys.

The Antilles were populated by river people from South America called the Tainos (the word hurricane is derived from the Tainos language), and by the later-arriving Arawak (collectively, the Caribe Indians). When Columbus landed in 1492 there were an estimated one million Tainos. Within 50 years, they were virtually exterminated, and the last surviving Carib Indians live on a reservation in Dominica.

CENTRAL AMERICA: The Connecting Link



The northern part of Central America (Belize and Guatemala to the Motagua Valley; Fig. 1.19) is similar to southern Mexico in topography, climate, and vegetation. Both are part of a terrane known as the Maya or Yucatán Block and belong to the North American Plate. The Motagua Valley of Guatemala represents the contact between the Maya Block and another terrane, the Chortis Block, as well as the contact between the North American and Caribbean plates. Middle Central America, or the Chortis Block, extends from the Motagua Valley to just south of Lago Nicaragua near the Nicaragua–Costa Rica border. The geographic features of northern and central Central America are due mostly to deformations resulting from the movement of the Maya and Chortis blocks, and later to the eastward movement of the Caribbean Plate and development of the Middle American Trench subduction zone (Chapter 2). Most of southern Central America (southern Costa Rica and Panama) formed from coalescence of volcanic islands and compression-extension forces developing from movements of the North and South American continents.

The climate patterns of Central America are determined primarily by (1) a low pressure system under the ascending arm of the Hadley convection cell, (2) the easterly trade winds, and (3) the polar trough that periodically brings cold air (nortes) as far south as Costa Rica. The climates are diverse, but they follow the usual pattern of warm and wet conditions in the tropical lowlands, cooler and moist environments at mid-elevations (and often very wet on the north- and east-facing slopes), and cooler and drier climates in the restricted highlands. Dry habitats may also occur to the lee of mountains, and on sites influenced by edaphic conditions, slope, or exposure. The MAT is 28° C at Choluteca (47 m elevation) in Honduras, and 14.4° C at Quetzaltenango (2500 m) in Guatemala. The greatest rainfall is in the lowlands and adjacent slopes such as at Limón, Costa Rica, with 3500 mm (3 m elevation); 3250 mm at Bocas del Toro (2 m elevation) and 3251 mm at Cristóbal (12 m elevation), Panama; and 3225 mm at Bluefields, Nicaragua (sea level). The lowest rainfall is at the higher elevations where moisture has been lost from the winds as they ascend the lower slopes. For example, it is 584 mm at Quetzaltenango (2500 m) in Guatemala. There is a climatic atlas that includes Central America (Steinhauser, 1979), and other climatic data for Central America are given in Table 1.2. Twenty-four fossil floras are used to describe the vegetation history of Central America (Fig. 6.1). The oldest is a small assemblage from Guatemala

of possible Cretaceous age. Others are from the Eocene of Panama through the Neogene of Guatemala, Costa Rica, and Panama. There are several Quaternary plant microfossil assemblages found from Belize to the Darién of Panama.

Guatemala

The physical features of Guatemala are mostly a continuation of three provinces described for southern Mexico (see Fig. 6.3). The Petén of northeastern Guatemala and much of Belize are extensions of the dry carbonate platform of the Yucatán Peninsula, and the mountains of western and central Guatemala represent a confluency of the Sierra Madre de Chiapas and the Front Ranges and High Plateaus of Mexico.

Northern Guatemala consists of a relatively flat, low, dry karst topography (the Petén) that makes up nearly one-half of the country. The Maya Mountains in the Petén are of moderate relief (~600 m) and extend westward into Belize. The principal mountain ranges outside the Petén are the Cordillera/Sierra de los Cuchumatanes in the west and the Sierra de Chuacús–Sierra de las Minas–Montañas del Mico across the central part of the country. The highest peak is Volcán Tajumulco at 4220 m in the Cordillera de los Cuchumatanes near the border with Chiapas, Mexico.

There is a relatively broad coastal plain along the Pacific Ocean rising from sea level to ~457 m elevation, and a more restricted low-lying area around Lago de Izabal and Puerto Barrios on the Atlantic coast. The major drainage systems are the Ríos Usumacinta, Polochic, and Motagua. The Río Usumacinta forms part of the boundary between Guatemala and

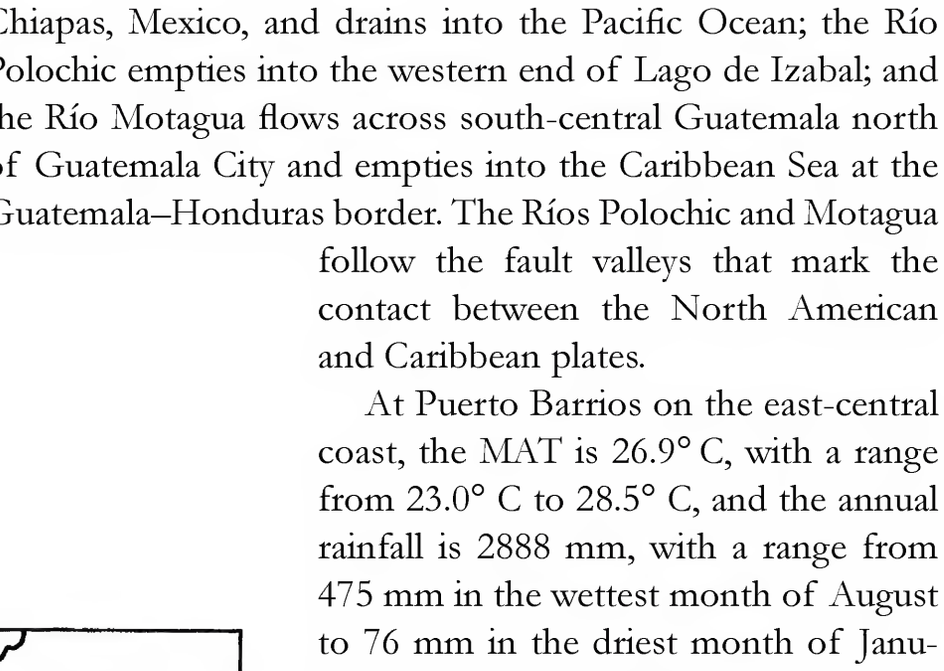


Figure 1.20. Four climatograms from the uplands of Guatemala. From Islebe et al. (1995).

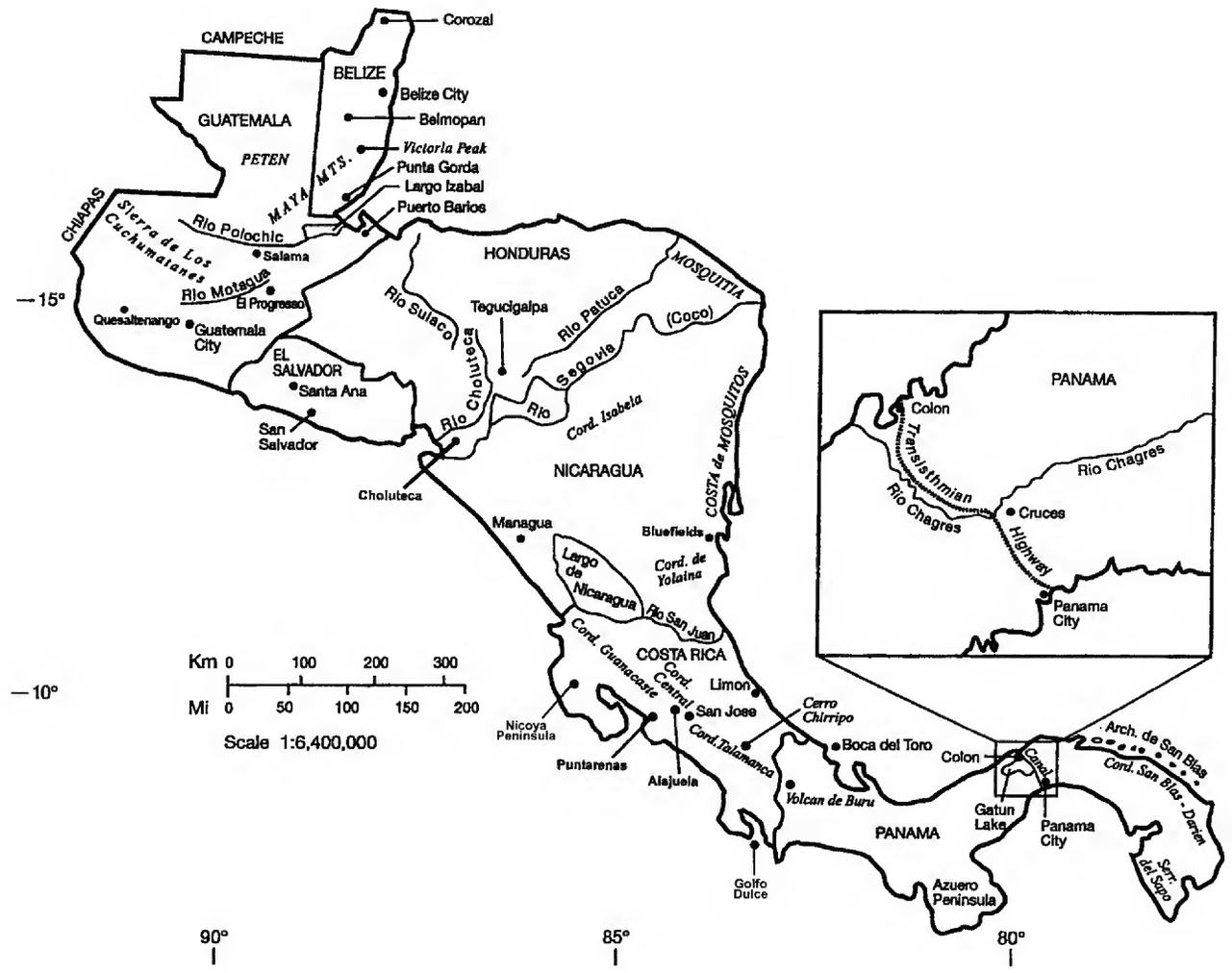


Figure 1.19. The countries and principal physiographic features of Central America referred to in the text.

Chiapas, Mexico, and drains into the Pacific Ocean; the Río Polochic empties into the western end of Lago de Izabal; and the Río Motagua flows across south-central Guatemala north of Guatemala City and empties into the Caribbean Sea at the Guatemala–Honduras border. The Ríos Polochic and Motagua follow the fault valleys that mark the contact between the North American and Caribbean plates.

At Puerto Barrios on the east-central coast, the MAT is 26.9° C, with a range from 23.0° C to 28.5° C, and the annual rainfall is 2888 mm, with a range from 475 mm in the wettest month of August to 76 mm in the driest month of January. In the Petén, MAT is ~25° C and annual rainfall averages 1600 mm. At the highest elevations of the Cordillera de los Cuchumatanes (3800 m), high temperatures reach 18° C in April and low temperatures drop to –3° C in January (Islebe et al., 1995). The MAP ranges between 1100 and 1800 mm at middle elevations, and decreases to 800 to 1000 mm at the summits (Garcia, 1987). The lapse rate is estimated at 5.5° C/km derived by incorporating some climate data from central Mexico (Lauer, 1973). Throughout Central America generally, the lapse rate is 5.9° C/km for elevations below 1500 m (Schwerdtfeger, 1976).

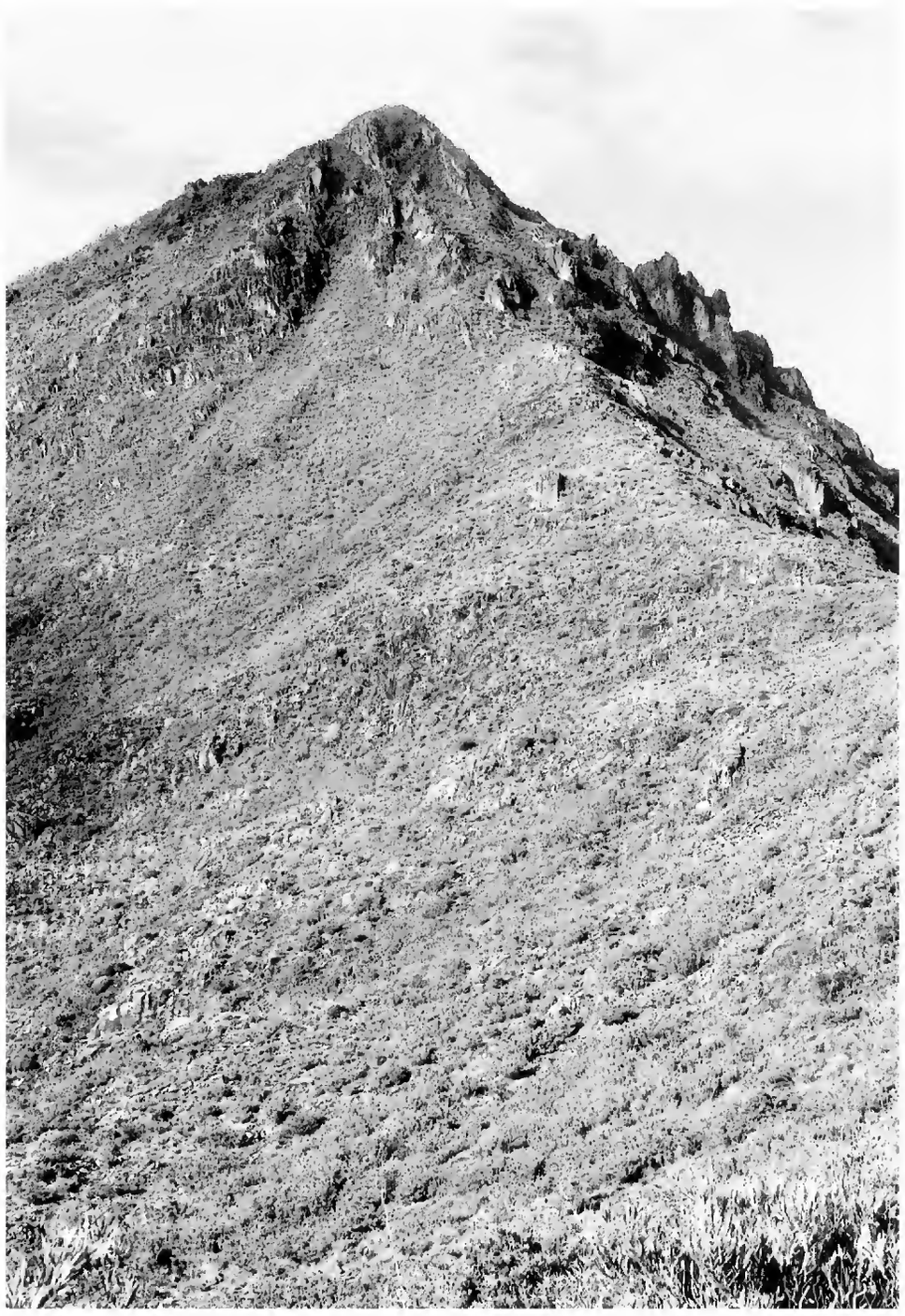


Figure 1.21. Cerro Chirripó, a glaciated peak at 3819 m in elevation, ~9°N latitude, south of San José in the Cordillera de Talamanca, Costa Rica. Photograph by Sally Horn.

Four climatograms for sites in the uplands are given in Fig. 1.20. Six fossil floras are found in Guatemala (Fig. 6.1), including one of possible Cretaceous age (two plants) from the Verapaz region. Palynofloras of Miocene and Pliocene age are known from the Padre Miguel Group and from the Herrería Formation in southeastern Guatemala, and there is an extensive database developing for the Quaternary of the lowland Maya region of the Petén. Spore and pollen studies, and associated vegetation transects, have also been made in the highlands of Guatemala (Chapter 6).

Belize

Early European settlers to Belize were British from Jamaica who came in 1622 to log mahogany, and in approximately 1800 they were recognized as a settlement under British protection from the Spanish. The northern part of the country belongs to the same dry and low carbonate platform as southeastern Mexico and northern Guatemala. In west-central Belize the Maya Mountains provide moderate physiographic relief up to an elevation of 1200 m at Victoria Peak. The Río Belize flows north of the Maya Mountains emptying into the Caribbean Sea at Belize City, and the Río Hondo forms the northern boundary with Mexico. Offshore ~25 km is the world's second largest barrier reef (after the Great Barrier Reef of Australia). Rainfall ranges from 1295 mm at Corozal in the north to 4445 mm at Punta Gorda in the south. A devastating hurricane in 1961 prompted relocation of the capital from coastal Belize City slightly inland to Belmopan. Spore and pollen assemblages of Quaternary age are known from northern Belize.

Honduras

Honduras consists of central highlands of low to moderate relief from which rivers flow onto the bordering coastal plains. The highest peak is the Cerro Las Minas at 2865 m in northwest Honduras adjacent to Guatemala, and the principal rivers are the Río Choluteca that flows into the Pacific Ocean and the Ríos Sulaco and Patuca that flow into the Atlantic Ocean. Valleys such as the Comayagua northwest of Tegucigalpa support a dry flora and fauna. It has been suggested they were once connected to form a subhumid corridor through northern Latin America, but the paleobotanical evidence suggests a mosaic of forest and shrubland. A notable feature of the country is the broad coastal plain and delta of the Río Patuca in the southeast called La Mosquitia. This region is bordered on the south by the Río Coco (also known as Río Segovia), which forms part of the boundary with Nicaragua. Some plant megafossils of Mesozoic (Jurassic) age are known from Honduras, but none have been described for the interval between the Late Cretaceous and Holocene.

El Salvador

El Salvador has the dubious distinction of being the most densely populated country in Latin America (as of 1996; Table 1.1). The Earth's population of an estimated one billion in 1800 reached six billion on Tuesday, 10 October 1999. The trend does not bode well for countries such as El Salvador, already burdened by overpopulation (Bongaarts & Bulatao, 2000; O'Neill et al., 2001; see reviews by Myers, 2001). Also, one effect of global warming appears to be intensifying El Niño and La Niña cycles in the low to middle latitudes, which will cause greater floods, drought, and severe hurricanes.

El Salvador is also one of the smallest countries of Latin America at 256 × 128 km, and in contrast to the hills and low mountains of Honduras, it is mostly low-lying coastal plain. The mountains that extend southward from Guatemala are mostly to the east of El Salvador, but they are the source of a few small rivers flowing across the country into the Pacific Ocean. Quaternary spores and pollen are known from lake sediments in the southern Maya area of El Salvador.

There are about 20 peaks of volcanic origin in El Salvador, and the highest is the Volcán de Santa Ana at 2381 m. On 13 January 2001 an earthquake of 7.6 magnitude occurred 65 miles southeast of San Salvador, and it was followed on 13 February by another of 6.1 magnitude about 15 miles east-southeast of the capital. There were more than 3000 aftershocks following the 13 January earthquake, and more than 1000 deaths were reported. The 2001 earthquake was the 14th

Figure 1.22. Lago Bonillita, Costa Rica. Photograph by Sally Horn.

to affect the capital in post-Columbian time. They are due to slippage of the Pacific Plate beneath the Caribbean Plate along the Middle American Trench.

Nicaragua

Nicaragua is the largest of the Central American countries (130,000 km^2, 12th in Latin America; Table 1.1)—about the size of Wisconsin in the United States. The principal river is the Río Coco (Río Segovia); the Río San Juan forms part of the southern border with Costa Rica; and Lake Nicaragua is the largest in Central America at 8430 km^2. For comparison, Lake Erie in the United States is 25,745 km^2. MAP in the dry valleys around Matagalpa in the Cordillera Isabella is 600 mm, the east-facing Atlantic slopes receive ~2400 mm, and the wettest sites along the Río San Juan receive 6000 mm. The Cordillera Isabella in northwestern Nicaragua is of middle-to-low elevation (Cerro Mogotón, 2107 m at the border with Honduras) and it continues southward as the Cordillera de Yolaina near the border with Costa Rica. The mountains near Bluefields are an important biogeographic zone marking the approximate southernmost distribution of several north-temperate trees. The vegetation includes *Pinus–Quercus* (pine-oak woods) with *Carpinus* (hornbeam, ironwood), *Juglans* (walnut), *Liquidambar* (sweetgum), and *Ulmus* (elm). The southernmost distribution of *Juniperus* (juniper) is just north of Bluefields. The region is tectonically active as witnessed by the 25 volcanoes between Tajamulca in western Guatemala and Volcán Barú in western Panama. In 1972, the capital city of Managua was leveled by an earthquake, and the decision of the Somoza regime to rebuild it on its family-owned land was a factor in the Sandinista rebellion and their eventual takeover in Nicaragua.

The low-lying Caribbean coastal plain of Nicaragua is known as the Costa de Mosquitos, named for the native population of the region, and it is a continuation of the Mosquitia region of adjacent Honduras. Only a single fossil plant (a legume, *Prioria tufficola*; Quaternary) has been published for the country. The same series of Tertiary volcanics in the highlands and lignites that mark the former coastlines in Veracruz and Chiapas, Mexico, and in Guatemala, continue along the eastern side of the central cordilleras to Honduras and Nicaragua. Megafossils preserved in ash are known to local inhabitants from mining and well construction, but no studies have been made. The sediments of Lago de Nicaragua must also preserve plant microfossils in a region in which the Quaternary vegetation and environmental history is essentially unknown.

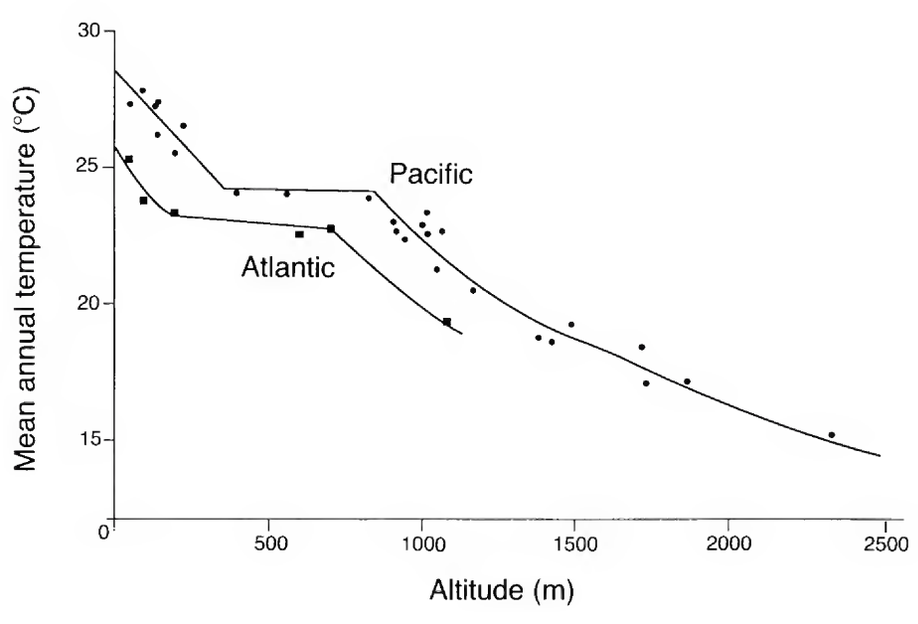


Figure 1.23. Annual temperature and altitude on the Atlantic and Pacific sides of Costa Rica. From Walsh (1996). Reprinted with the permission of Cambridge University Press.

Costa Rica

One of the differences between the geography of Costa Rica and that of Nicaragua and Honduras is the presence of more extensive highlands in Costa Rica. The principal mountain chains are the Cordillera de Guanacaste in the north (Volcán Miravalles, 2020 m; Volcán Rincón de la Vieja, 1920 m), Cordillera de Tilarán (highest peak Cerro los Amigos, 1842 m), the

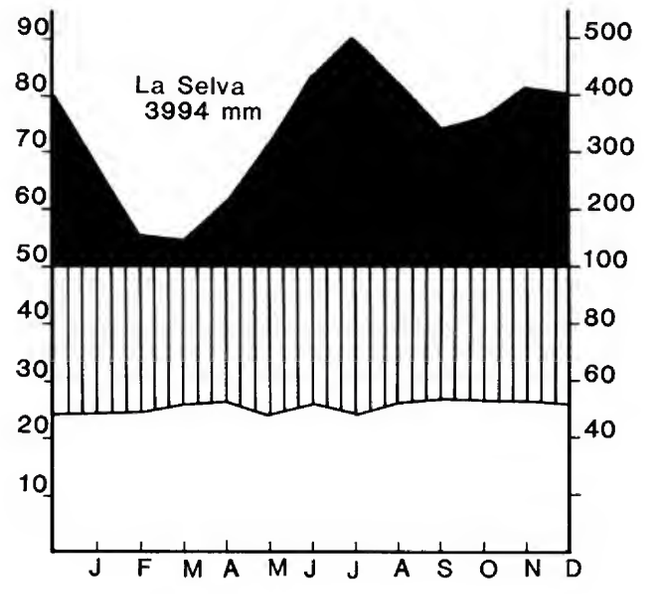


Figure 1.24. Climatogram from La Selva, Costa Rica. From Gentry (1990), used with permission of Yale University Press, New Haven, Connecticut.

Cordillera Central around the Meseta Central (Volcán Irazú, 3428 m; Volcán de Turrialba, 3328 m), and the Cordillera de Talamanca in central and southern Costa Rica (Grayum et al., 2004). The highest peak in Costa Rica is the glaciated Cerro Chirripó at 3819 m in the Cordillera de Talamanca (Fig. 1.21). The largest valleys are the Meseta Central in which the capital of San José is located, and the Valle de General, south of the Cerro de la Muerte. One reason for the difference in topographic diversity is that the two regions from central Guatemala to northern Costa Rica, and from about central Costa Rica through Panama, had separate geological histories. The former on the Chortis Block has highlands generated mostly in the Cretaceous. The highlands of southern Central America are younger and developed primarily in the Miocene between 12 and 10 Ma from subduction of the Cocos Ridge beneath the Caribbean Plate along the Middle American Trench and, to some extent, from compression forces generated by movement of South America toward North America. The landscape was modernized in the Quaternary by erosion and glaciation, with the formation of numerous lakes in the Cerro Chirripó region (e.g., Lago Bonillita; Fig. 1.22).

Representative climatic data for Costa Rica are given in Table 1.2, and data for other locations are provided by Coen (1983), Herrera (1985), Sanford et al. (1994; La Selva), and Clark et al. (2000; Monteverde). MAT is 26.8° C at Puntarenas (elevation 3 m) and 19.5° C at San José (elevation 1200 m; Table 1.2; Figs. 1.23, 1.24). The average lapse rate is ~5.9° C/km (Fig. 1.23). On the peak of Chirripó, the maximum temperature is ~7.2° C, the minimum is 2.2° C, producing frequent frost but no permanent ice, and the lapse rate is 5.4° C/km. The rainy season is from about May to October, following the migration of the ITCZ on the Pacific side with a lag time of about two months. The highest precipitation is at middle elevations along the Atlantic east-facing slopes of the central mountains from the northeast trade winds (strongest from November to April) ascending the central cordilleras, where the annual rainfall may be >5000 mm. The amounts and seasonal distribution of rainfall are relatively consistent in southern Central America because hurricanes are infrequent. In the past 100 years, only one (Martha, 21–25 November 1969) directly affected Costa Rica (Coen, 1983).

As with many places in the tropics, the difference between the warmest and coldest months in the lowlands (~5° C in Costa Rica) is exceeded by the diurnal (daily) variation because of nightly cold air drainage from the mountains along valleys into the lowlands. At La Selva Biological Station (10°26'N, 83°59'W; Fig. 1.24), the daily range is 6°–12° C compared to the cold-versus-warm-month averages of <3° C (McDade et al., 1994). Thus, in times before the principal uplift of the central cordilleras in the Mio–Pliocene, the more subdued topography likely augmented the relatively uniform temperatures of southern Central America resulting from the low-latitude position and the near-maritime environment of most of the region. Janzen (1967) suggests that mountains in the tropics are more formidable barriers to migration than those in temperate regions because lowland organisms in the tropics are not as adapted to the wide changes in temperature as those in the temperate zones. Another observation is that in forests along Río Potrero in Guanacaste Province, the mid-morning

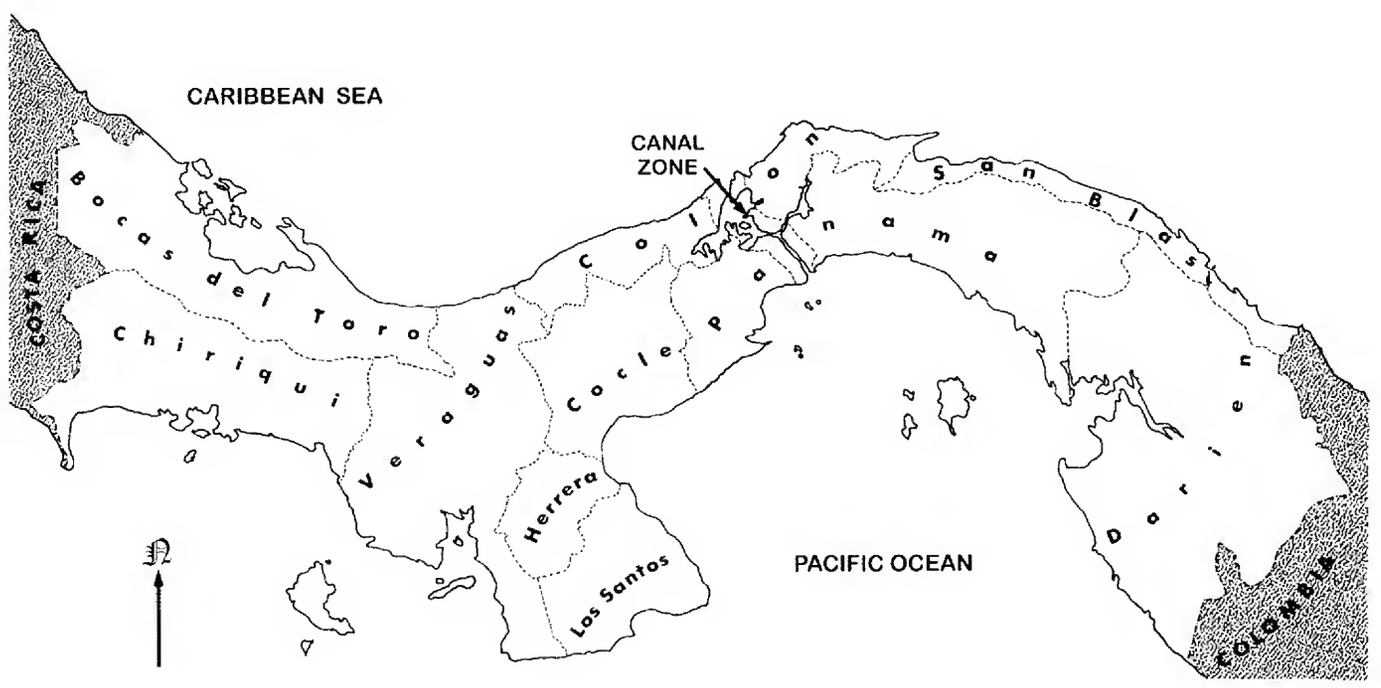


Figure 1.25. The political subdivisions of Panama. From Porter (1973).

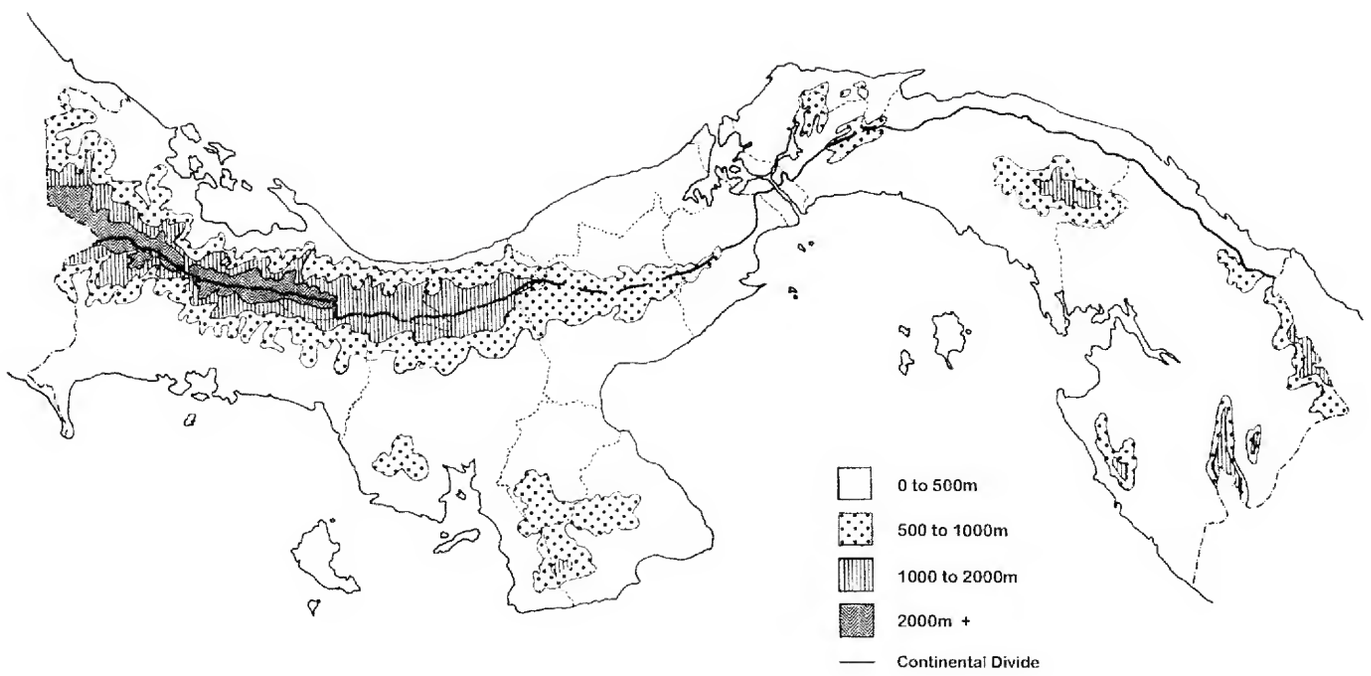


Figure 1.26. The elevations of Panama. From Porter (1973), based on Myers (1969).

Figure 1.27. Balboa Heights, Sosa Hill, and the Interamerican Bridge from the steps of the Administration Building of the Panama Canal Company. The Interamerican Bridge, inaugurated on Columbus Day, 12 October 1962, is the overland route connecting the North and South American continents after completion of the canal.

air temperature is 29.6° C and supports lush subtropical vegetation, while in the adjacent uplands the temperature is 35.3° C, the relative humidity is 30% lower, and the vegetation is deciduous forest (Janzen, 1967). This quantifies the well-known observation that gallery forests often support the most tropical vegetation. Extending this observation into past times, it suggests that similar habitats preserved tropical vegetation the longest during drying climatic cycles, and that the net biological inventory of a region begins to increase with the principal period(s) of orogeny. Fossil palynofloras of Neogene age (Miocene–Pliocene) are known from eastern Costa Rica, and others of Quaternary age are known from lakes and bogs at several sites (e.g., Lago Bonillita; Fig. 1.22).

Figure 1.28. *Rhizophora mangle*, Interamerican Bridge, Panama.

Figure 1.29. Miraflores Lock, Panama Canal. The first commercial traffic through the canal was on 15 August 1914, reducing travel from New York to San Francisco from 13,000 to 5000 miles. Tolls are calculated by weight. On 25 January 1980, the *R.M.S. Queen Elizabeth 2* paid $89,154.62, and on 2 May 1997, the *Crown Princess* paid $141,344.97. The lowest toll was 36 cents, paid by Richard Halliburton, who swam the canal in 1928.

Figure 1.30. The Río Chagres, Panama.

Panama

Panama is the narrowest link between South America and Central/North America (Figs. 1.25–1.28). It is 672 km long, 189 km across the widest point, and only 48 km across the narrowest point near the Panama Canal (Fig. 1.29). The principal mountains are the Cordillera Central in the west, a continuation of the Cordillera de Talamanca of Costa Rica, and the Cordillera de San Blas in the east that continues southward as the Serranía del Darién. The Serranía del Sapo is a series of low hills along the southern Pacific coast of the Darién. The highest peak in Panama is Volcán Barú or Chiriquí in the northern part of the Cordillera Central at 3475 m. The Serranía de Tabasará reaches 2826 m at Cerro Santiago, while the Cordillera de San Blas, Serranía del Darién, and Serranía del Sapo are mostly less than 1500 m. There are Atlantic and Pacific coastal plains, with some 1600 islands along the coasts such as the archipelagoes of Bocas del Toro in the north and San Blas in the south, and much of the Darién Province near the Colombia border is near sea level. The Spanish name of Santa María de l'Antigua del Darién was given to the region by Balboa, who had moved there to escape attacks from the natives, and so established the Spanish presence in Panama. It was from Panama that the Spanish launched the expedition that led to the European discovery of the Pacific Ocean.[8]

One of the historic rivers of Latin America is the Río Chagres (Minter, 1948; Fig. 1.30). It was dammed to form Gatún Lake as a waiting area for ships passing through the narrow, 12.9-km-long Gaillard Cut of the canal. Hilltops were converted into islands by the rising waters, and one of these, Barro Colorado Island, serves as a biological station for the Smithsonian Tropical Research Institute (STRI; Fig. 1.31). The laboratories and offices of STRI are located in the former Canal Zone on the earlier site of the historic Tivoli Hotel (Fig. 1.32). As with the biological stations and reserves elsewhere in Latin America, the preservation and detailed knowledge of the biology of Barro Colorado Island, along with extensive data on the geology and climatology of the former Canal Zone, greatly facilitates tracing the history of the biota in southern Central America. A fascinating account of the travails and intrigue involved in acquiring the land, originally belonging to Colombia, and in constructing the canal, is given by McCullough (1977).

Panama is centered mostly between 8° and 11°N, and the climate is influenced by the seasonal meandering of the ITCZ in the eastern Pacific Ocean. It shifts south in January–February from near the equator to 2°–3°S, and north in June–July to about the latitude of Panama. In the Pacific lowlands, the wet season is from May through December, and the dry season, which may be relatively pronounced (less than 5 cm/mo; up to two months without rain) extends from about January through April. At this low latitude, annual temperature varies within a narrow range of only a few degrees (Fig. 1.33). The low elevation and narrow dimensions of the land between the Caribbean Sea and the Pacific Ocean further buffer Panama against significant changes in temperature. The MAT at Cristóbal (elevation 12 m) is 27° C, and it is about the same at Santiago (elevation 90 m) and David (27 m) to the west. Rainfall is greater along the Atlantic coast at 1500–3000 mm than along the Pacific coast at 1140–2290 mm. The weather in Panama, as elsewhere, is affected by El Niños, and one effect is that drought drops the navigable depth of the Panama Canal from 40 ft to 34 ft. This reduces ship traffic by 17%, and it is an event of considerable economic and strategic importance.

Eight fossil floras have been described for Panama (Fig. 6.1). The oldest are plant microfossils of Eocene age, and others of Miocene age, from central Panama. Quaternary assemblages are known from the west near the border with Costa Rica, to the east in the Darién near Colombia, and from cores in Gatún Lake.

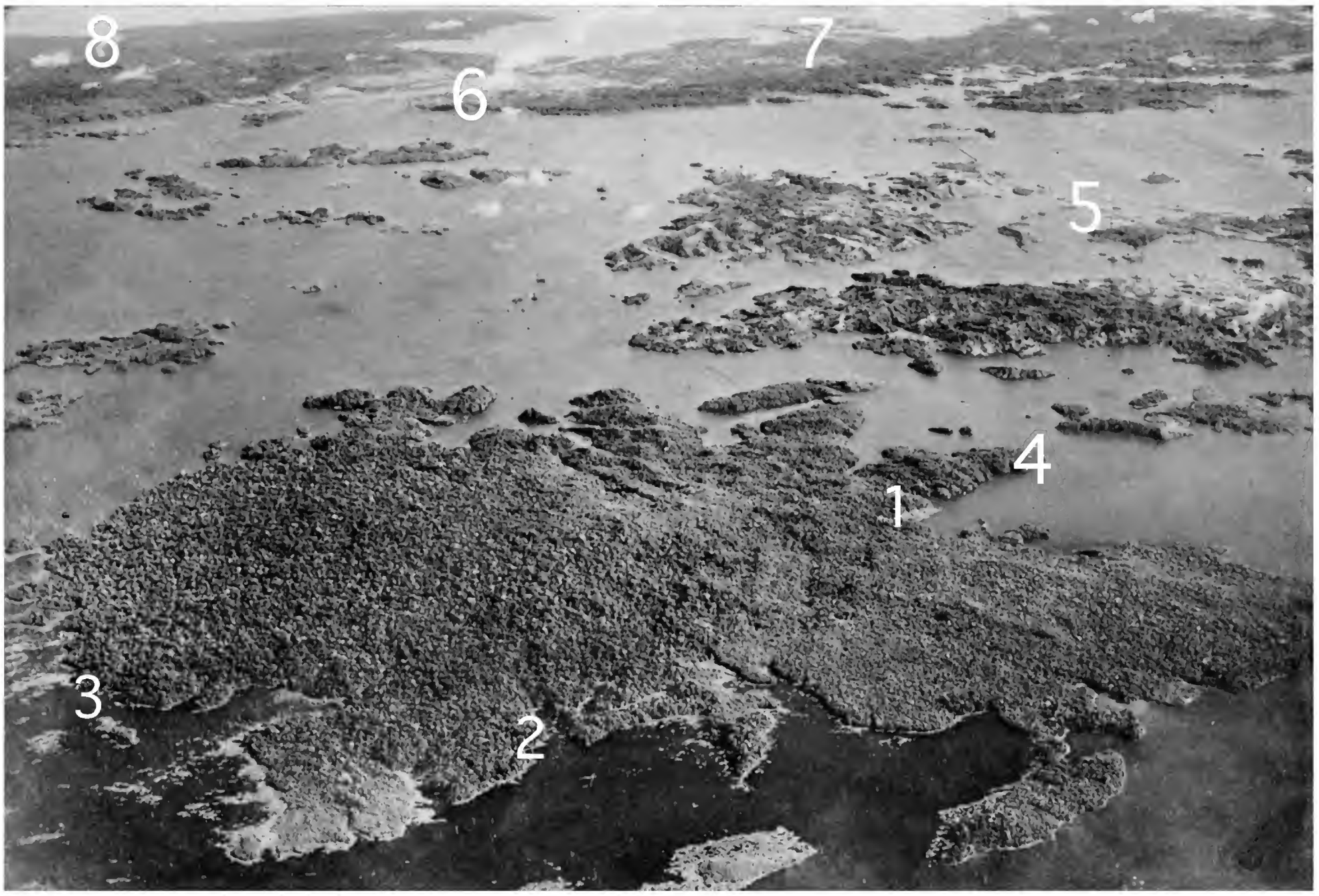


Figure 1.31. Barro Colorado Island in Gatún Lake, Panama. 1 = Laboratory clearing, 2 = Termite house, 3 = Redwood House, 4 = Fairchild Point (the Canal passes this point), 5 = Monte Lirio on the Panama Railroad, 6 = Gatún, 7 = Cristóbal, 8 = mouth of the Chagres River. From Chapman (1929).

Figure 1.32. The Tivoli Hotel, former Canal Zone, Panama. One wing of the hotel was rushed to completion to house its first guest, Theodore Roosevelt, who arrived in Panama for an inspection trip of the canal on 14 November 1906. The hotel was torn down in 1971, in part because of termite damage, and the site is now occupied by the Smithsonian Tropical Research Institute (STRI).

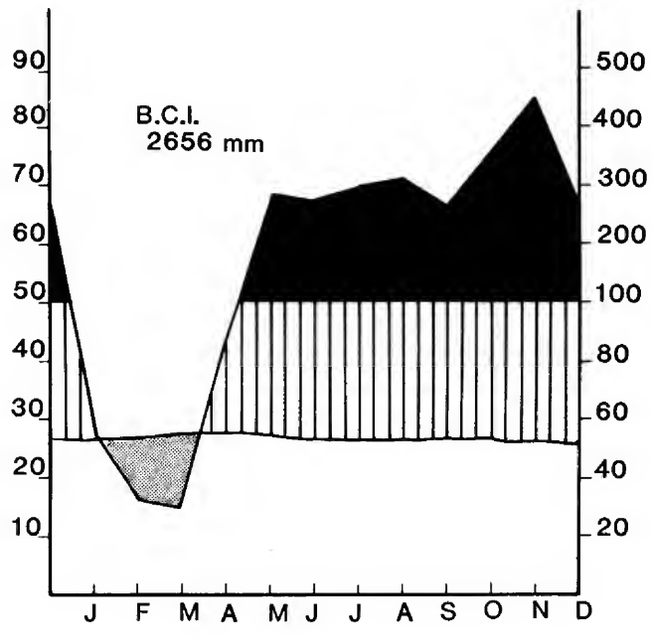
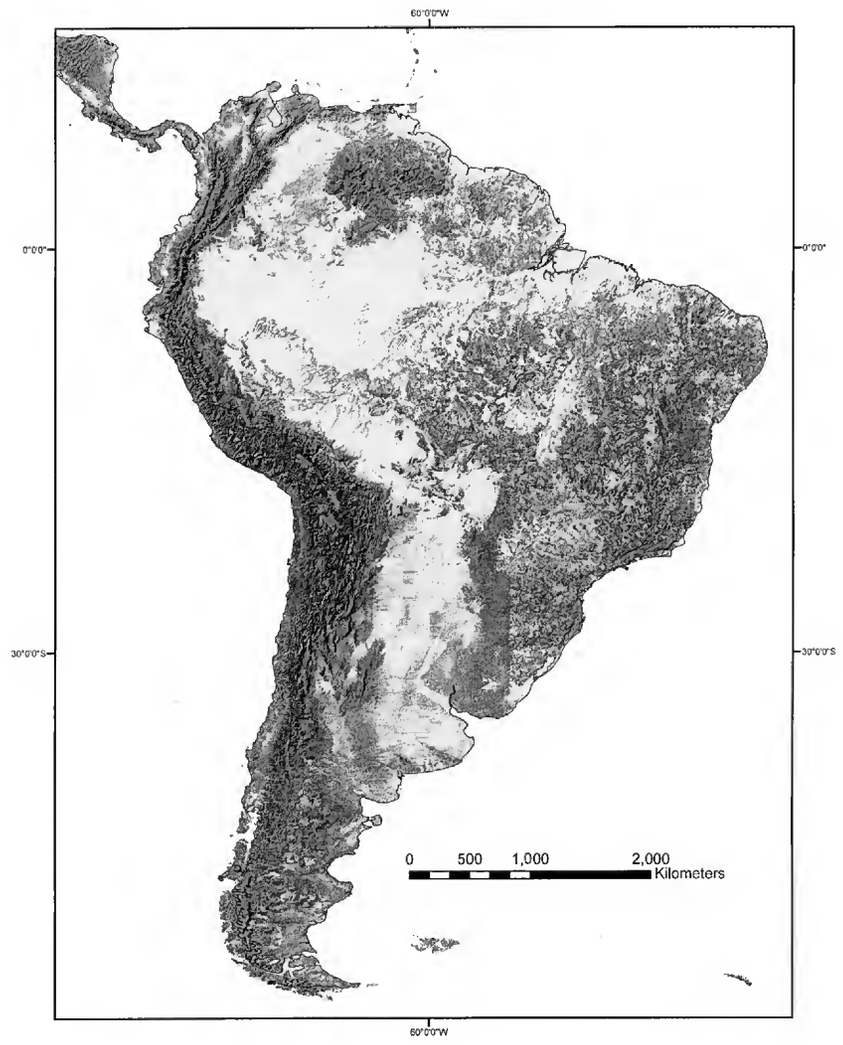


Figure 1.33. Climatogram for Barro Colorado Island, Panama. From Gentry (1990). Used with permission of Yale University Press, New Haven, Connecticut.



A characterization of the geography of the vast continent of South America most relevant to a survey of vegetational history and terrestrial paleoenvironments can be organized around two of its most prominent physical features—the Andes Mountains (including the adjacent slopes) and the low-lying basins (Figs. 1.34, 1.35). As South America was forced westward by spreading from the Mid-Atlantic Ridge, several related geologic processes affected the western margin of the continent. There was deformation as lighter continental rock was pushed against denser oceanic basalt and plate ridges; uplift and volcanism as the leading edge of the heavier Pacific Plate subducted under South America; accretion as the relative westward movement of South America appressed volcanic island arcs and other materials and structures against the western coast; and shearing as the Caribbean Plate slid past northern South America. One result of these processes, operating since the separation of South America from Africa beginning 160 Ma, is the Andes Mountains extending over 8000 km along the western coast. Various segments of the mountain chain have had different geologic origins (Chapter 2). For convenience of reference and in recognition of the geologic differences, three physiographic provinces are recognized—the northern, central, and southern Andes. Within each province, faulting, compression, and extension forces have further created highland valleys such as those of Bogotá, Colombia; Quito, Ecuador; Junín, Ayacucho, and Cuzco, Peru; and La Paz and Cochabamba, Bolivia. These valleys contain thousands of feet of sediments eroded from the adjacent slopes, and they have been the sites of numerous paleontological studies in South America. The Andean countries include Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, and Argentina.

At the same time that Precambrian and younger surface rocks were being flexed upward to form the core of the Andes Mountains and other highlands, broad depressions developed to constitute the great lowland basins of South America. They also have become mostly filled by erosion products from the Andes Mountains and the Guayana and Brazilian shields, such as the 4000 m of sediment that now occupy Amazonia. The Amazonian countries are Guyana, Suriname, and French Guiana to the north, Paraguay and Uruguay to the south, and Brazil centered in the expanse of the Amazon Basin. In discussing the geography of South America, emphasis is placed on those physiographic features most relevant to the geology (Chapter 2), modern vegetation (Chapter 3), and paleocommunities (Chapters 4–7).

General climate data for the continent are given in Figs. 1.36–1.38, and for representative sites in each country in Table 1.2. Haack (1985) has published a series of maps showing January–July temperatures, average annual precipitation, atmospheric pressure, wind directions, ocean currents, and Walter climatograms for Quito, Ecuador; La Paz, Bolivia; Iquique, Santiago, Puerto Montt, and Punta Arenas, Chile; and Manaus, Corumbá, and São Paulo, Brazil. Climatograms for other places are given in the text.

The climates of the equatorial Pacific Ocean, together with the Indonesian region and a cell extending from Senegal across Africa to the Indian Ocean, are part of a weather system known as the Walker circulation. This system of alternating highs and lows (convection and subsidence) determines the annual see-saw pattern of wet monsoon and dry season

Figure 1.34. Political subdivisions of South America.

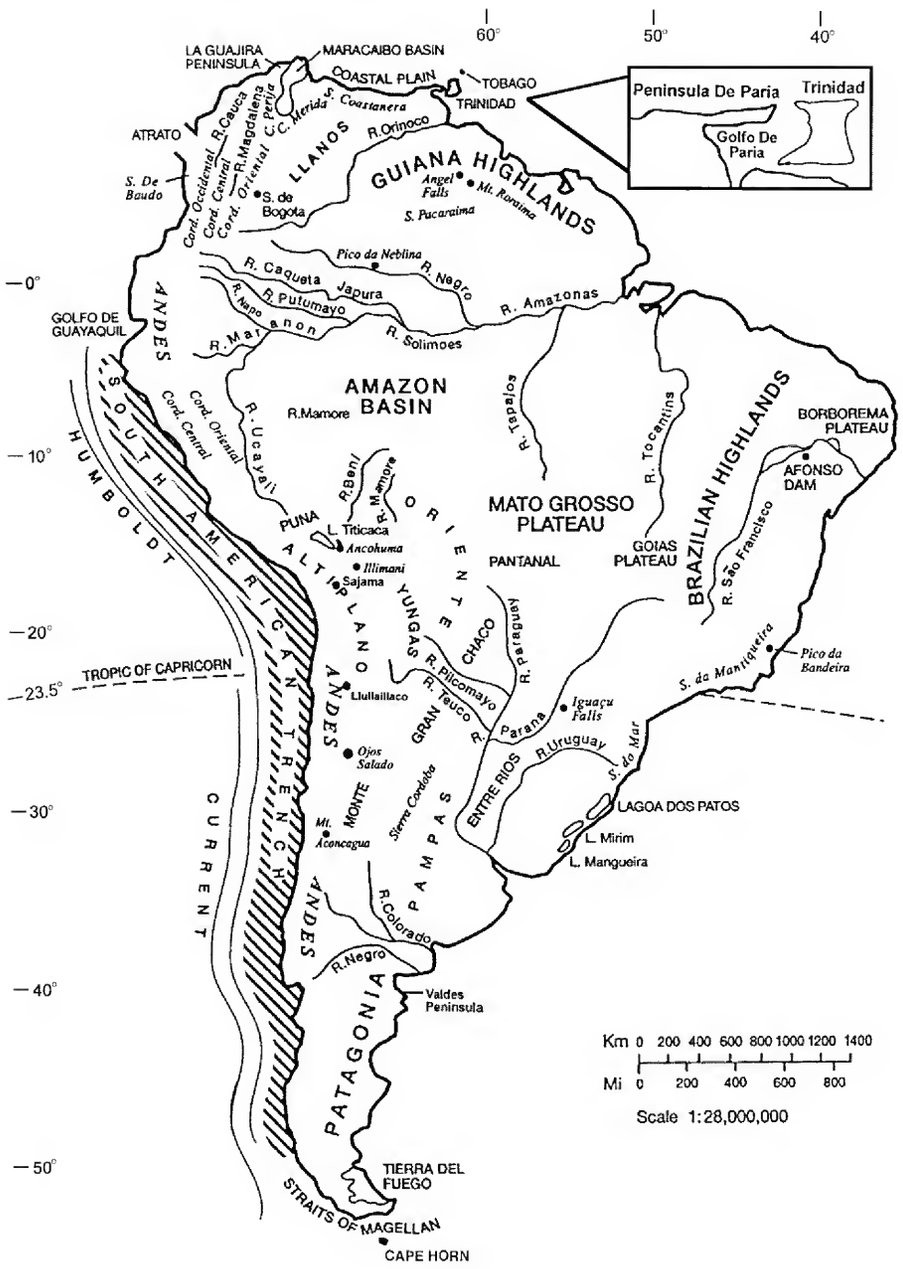


Figure 1.35. Principal physiographic features of South America mentioned in the text.

precipitation across the low and middle regions of the Earth. Changes brought about by mountain building, continental movement, ocean circulation, or insolation alter the Walker circulation–regional climates–vegetation, and ENSO events are part of the system (El Niño–Southern Oscillation; for more information, visit the Center for Ocean-Atmospheric Prediction Studies Library Web site [http://www.coaps.fsu.edu/lib/biblio/walker-circ.html]).

The Late Cretaceous through Cenozoic fossil floras studied for South America are numerous but unevenly distributed over a vast geographic area. For example, there are few or no large, recently studied, published fossil floras for Ecuador, Paraguay, Peru, or Uruguay. In contrast, there have been numerous investigations on the Quaternary of the high northern and central Andes Mountains (Colombia, Bolivia) and in the region of Chile–Patagonia–Southern Andes Mountains, but only seven in the Amazon Basin extend into the Last Glacial Maximum (LGM). Approximately 200 studies and 5200 taxa are reviewed here for the Cretaceous and Cenozoic of South America (Tables 7.1, 7.2, 7.6).

Venezuela

> "I am convinced that it is the spot of the earthly paradise [Eden] whither no one can go but by God's permission…I do not suppose that the earthly paradise is in the form of a rugged mountain, as the descriptions of it have made it appear, but that it is on the summit of the spot which I have described… I think also that the water I have described [the Orinoco] may proceed from it, though it may be far off, and that stopping at the place which I have just left, it forms this lake [the Gulf of Paria]. There are great indications of this being the terrestrial paradise, for its site coincides with the opinion of holy and wise theologians, and, moreover, the older evidences agree with the supposition, for I have never either read or heard of fresh water coming in so large a quantity in close conjunction with the water of the sea. The idea is also corroborated by the blandness of the temperature; and if the water of which I speak does not proceed from the earthly paradise, it seems to be a still greater wonder, for I do not believe that there is any river in the world so large or so deep." (From the log of the third voyage of Christopher Columbus, 1498; quoted from Boorstin, 1983, p. 242)

On his fourth and last voyage in 1502, Columbus visited Cuba, which he still thought was China, then sailed along the coast of Central America looking for the elusive strait used by

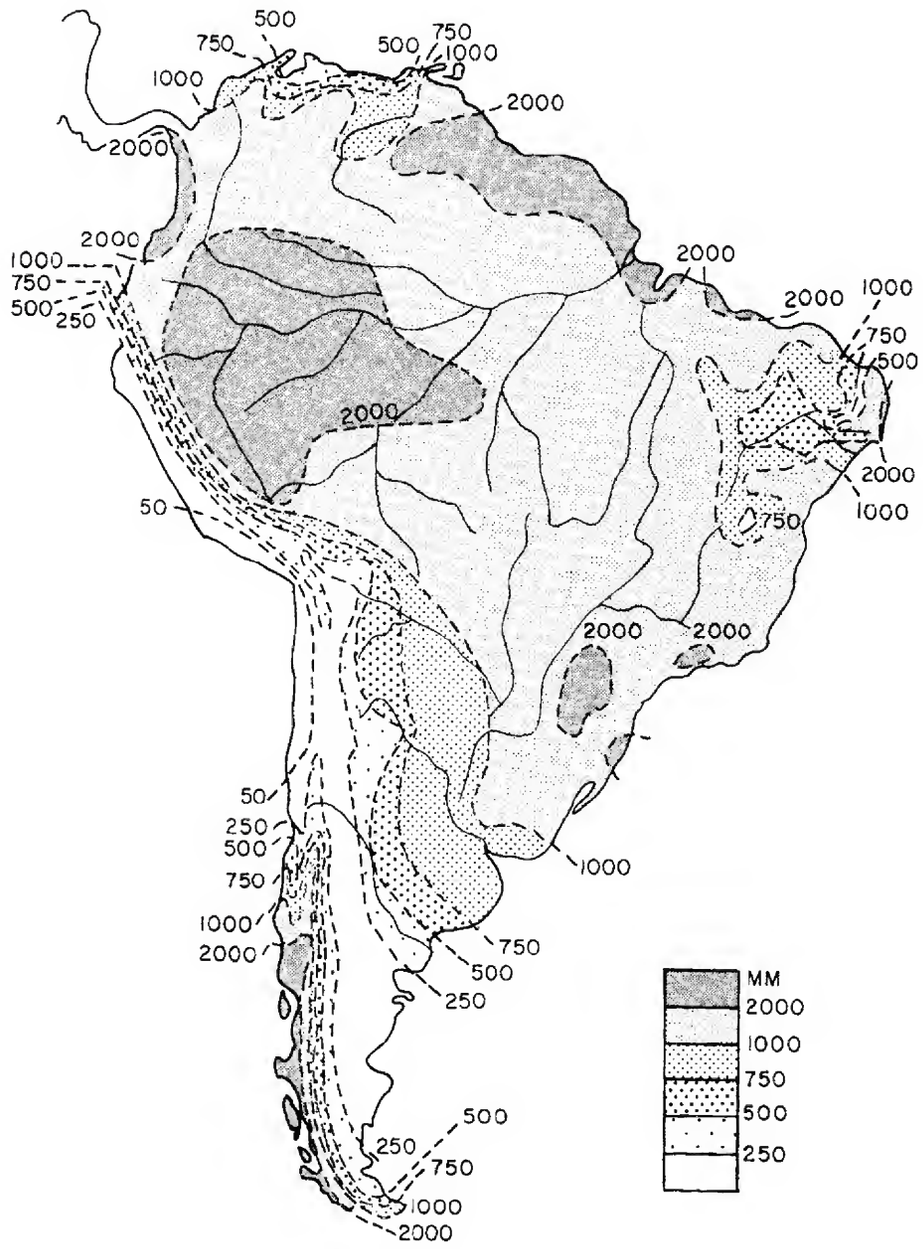
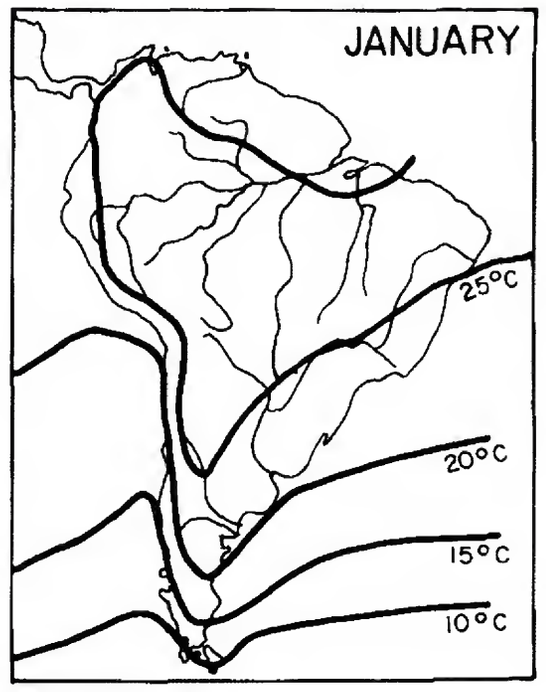


Figure 1.36. Mean annual precipitation for South America. Reprinted from Clapperton (1993), with permission of Elsevier Science Publishers, Amsterdam.



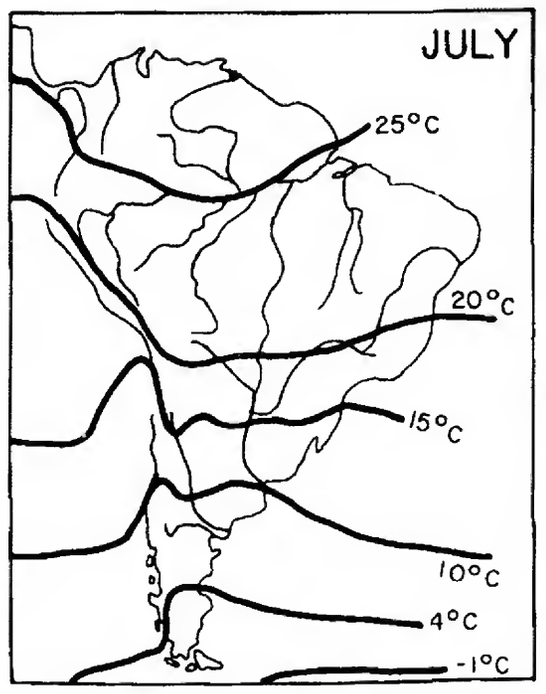


Figure 1.37. Mean annual temperature for January and July for South America. Reprinted from Clapperton (1993), with permission of Elsevier Science Publishers, Amsterdam.

Marco Polo to sail from China into the Indian Ocean. Columbus died in 1506 believing that on all four voyages, he had been sailing along the coast of eastern Asia. The recognition that South America represented a continent previously unknown to the Europeans belongs to Amerigo Vespucci. On his voyage from Lisbon beginning on 13 May 1501, he noted that "we arrived at a new land which, for many reasons that are enumerated in what follows, we observed to be a continent" (quoted from Boorstin, 1983), and when Gerardus Mercator published his map of the world in 1538 it showed for the first time the North American and the South American continents. Dominican friars established a colony at Cumaná on the northeastern coast of Venezuela in 1513, nearly 100 years before the settlement at Jamestown, Virginia, in 1607. Other early centers were the island town of Curaçao founded in 1520, Coro in 1527, Mérida in 1558, San Cristóbal in 1561, and Caracas in 1567.

Five physiographic provinces are recognized for Venezuela—the Andes Mountains, the Maracaibo Basin, Los Llanos (Los Llanos Orientales; Orinoco River floodplain), the Orinoco Delta and Coastal Plain, and the Guayana Highlands.[9] In southwestern Colombia, the Andes Mountains branch northward to form the Cordillera Occidental, Cordillera Central, and Cordillera Oriental. The Cordillera Oriental further branches into an eastern range (Cordillera de Mérida or Sierra Nevada de Mérida) and the western ranges of the Sierra Nevada de Santa Marta and the Sierra de Perijá that form the western boundary with Colombia. The Cordillera de Mérida includes the highest peaks in Venezuela—the glaciated La Columa or Pico Bolívar at 5007 m (Schubert, 1972) and Pico Humboldt at 4938 m. Across the northern end of the Cordillera de Mérida are the smaller Serranía Costanera (average elevation 1219 m) and the Serranía Interior. The highest elevation in the latter is Naiguatá Peak near Caracas at 2765 m. The region to the east of the Cordillera de Mérida is the Central Highlands, which includes the Valencia Basin. The sediments of Lake Valencia preserve plant microfossils of Quaternary age that have proven particularly useful for studying climatic change at the glacial–interglacial transition (Chapter 7). The mountains along the north coast of South America extend from the Cordillera de Mérida to Tobago and the Northern Range of Trinidad. Collectively

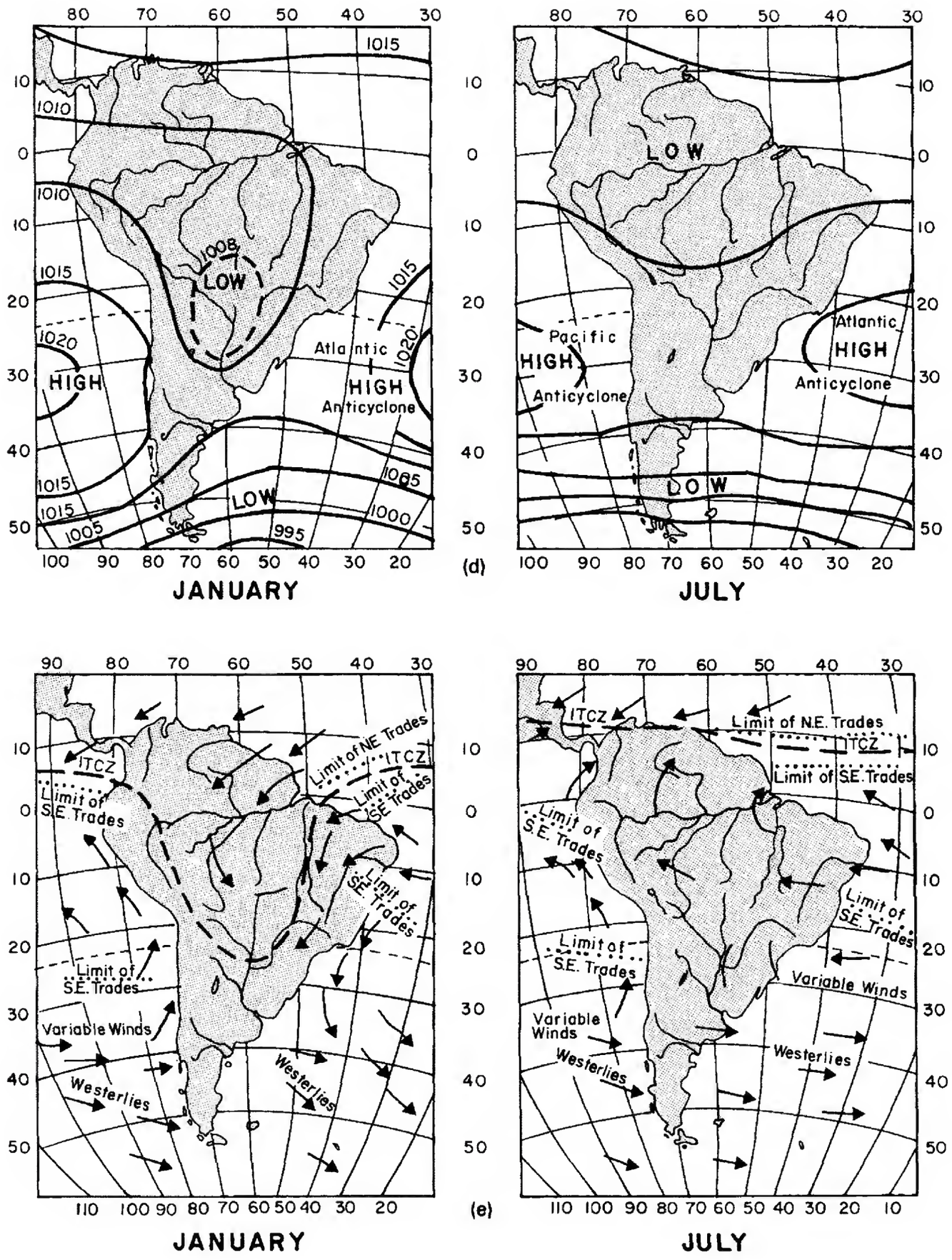


Figure 1.38. Average atmospheric pressure at sea level (top) and average air flow (bottom) for January and July for South America. Reprinted from Clapperton (1993), with permission of Elsevier Science Publishers, Amsterdam.

they are known as the Caribbean mountain system (or Cordillera del Norte), and the islands off the northern coast of South America are emerged peaks of these mountains. Further offshore from central Venezuela is the Cariaco Basin, which is becoming a center for innovative studies on Neotropical paleoclimate. Titanium is a terrestrial mineral brought into marine basins by rivers, and fluctuations in the amounts transported are a measure of river flow (viz., precipitation). Studies have confirmed correlation of past dry intervals in the Caribbean region with events of biological interest, such as the collapse of the lowland Maya civilization, and a variable association of dryness with cold periods in the lowlands during the Quaternary (Chapter 8).

The MAT is 28.5° C at Maracaibo (near sea level), 21° C at Caracas (elevation 1000 m), and 18° C at Mérida (1700 m) for a lapse rate of ~6.1° C/km. In Caracas the annual precipitation is 800 mm with a dry season from January through March (25.4 mm/mo) and a wet season from June through October (102 mm/mo). In the drier La Guajira and Paraguana peninsulas, the annual rainfall averages 304.8 mm, and along their southern coasts it is 135–250 mm.

The Maracaibo Basin (50,000 km^2) with Lake Maracaibo (15,000 km^2, maximum depth 35 m), the largest in South America, is an inlet situated between the Sierra Nevada de Santa Marta on the west and the Cordillera de Mérida on the south and east. The modern development of Venezuela and the detailed information available on its local geology are, in part, results of the hydrocarbon reserves in the Maracaibo

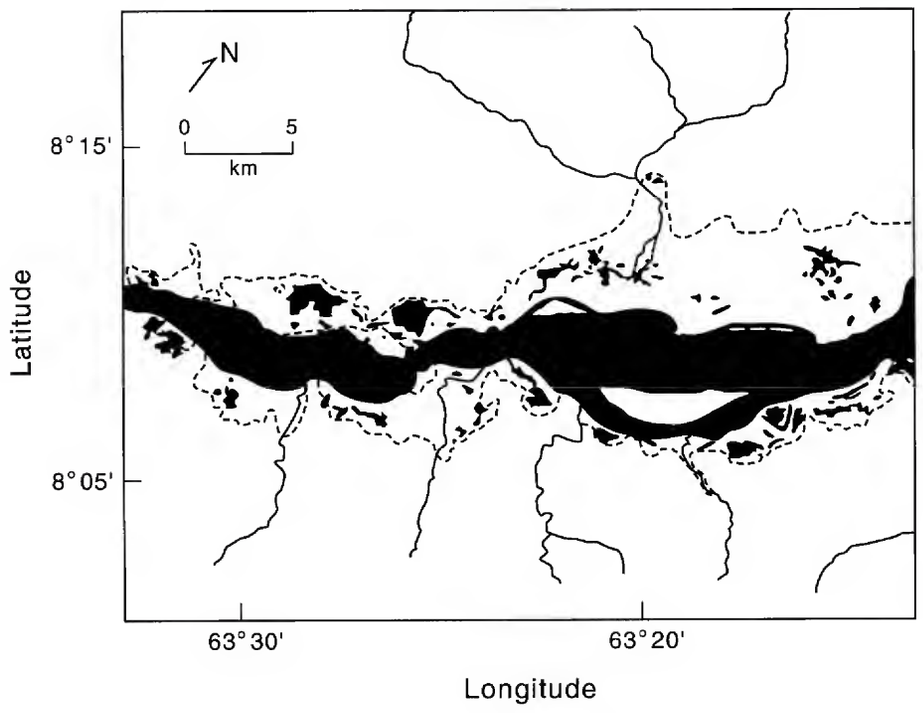


Figure 1.39. Portion of the Orinoco River floodplain showing permanent standing water (black) and maximum flooding (dotted lines). From Lewis et al. (2000). Copyright, American Institute of Biological Sciences.

Basin. The need for information on the age, depositional environments, stratigraphic correlation, and zonation of the oil-bearing deposits has generated numerous palynological studies on late Mesozoic and Cenozoic sediments, initially by personnel of the Dutch Shell Oil Company and later by members of Venezuela's Petróleos de Venezuela. Thus, the plant microfossil record in northern Venezuela is well known, although because of the applied nature of the studies, an artificial system of nomenclature is mostly used, rather than one based on the biological affinities of the specimens. This limits their use in tracing lineage histories, biogeography, and paleoecology.

Los Llanos—The largest river system in Venezuela is the Orinoco, which originates from tributaries to the north and west in the Andes Mountains and from the south and east in the Guayana Highlands. It is the world's third largest river as measured by discharge (38,000 m^3/sec) after the Amazon River, which is five to six times larger, and the Nile-Zaire River, which is slightly larger (Lewis et al., 2000). The area drained by the Orinoco River (Fig. 1.39) is 1.1 million km^2 with ~2300 shallow basins each consisting of open-water lakes with surrounding floodplain forests.

During the middle of the rainy season from June through October, about 80% of the floodplain is flooded forest, 10% is open water, and 10% is covered by macrophyte mats. These mats are made up mostly of the aquatic grass *Paspalum repens* and support populations of invertebrates that may reach 100,000 individuals/m^2. The grass stems elongate rapidly enough to keep up with local floodwaters that can rise 10–15 m annually.

The broad plain of the Orinoco River between the Cordillera de Mérida and the Guayana Highlands is called Los Llanos, constituting essentially the state of Bolívar.

Los Llanos is the largest savanna in tropical America and is mostly a low-lying rolling landscape with forest along the river. The river flows into the Atlantic Ocean forming a broad delta between Caripito and San José de Amacuro. The delta sediments contain pollen and spores transported by the river into the coastal basin of deposition. These have been used to reconstruct the paleovegetation, study differential preservation, the quantitative and qualitative aspects of the fossilization process (taphonomy), and establish the physical, climatic, and depositional environments of the deltaic sediments in which much of the hydrocarbon reserves of northern South America are preserved.

Guayana Highlands, Tepuis, and the Gran Sabana—To the east of Los Llanos are the sparsely populated Guayana Highlands, which constitute about 50% of Venezuela. The highest peak is Mount Roraima (2810 m). The southern margin of the highlands is the Serra Pacaraima, which forms part of the border with Brazil. MAP is from a maximum of 3000–4000 mm to between 1000 and 2000 mm, MAT is ~24° C below 1400 m and 8°–12° C above 2400 m, and the lapse

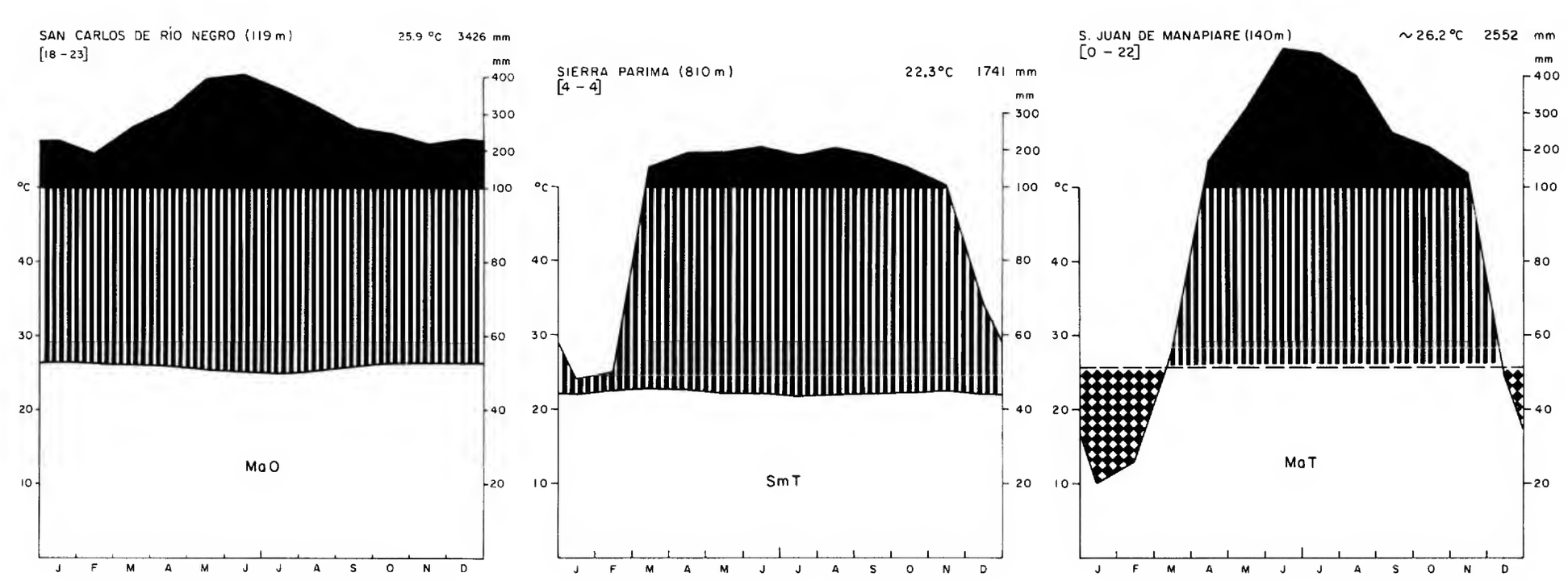


Figure 1.40. Climatograms for three sites in the Venezuelan Guayana. From Steyermark et al. (1995). Used with permission of Missouri Botanical Garden, St. Louis/Timber Press, Portland, Oregon.

rate is 6° C/km. Climatograms for various sites in the Venezuelan Guayana are shown in Fig. 1.40. In this region there are steep-sided, flat-topped mesas called tepuis (Fig. 1.41). These isolated structures emerging from the mist and forest to an elevation of ~2700 m were the setting for Sir Arthur Conan Doyle's novel, *The Lost World*. MAT at the base of Chimantá tepui in the state of Bolívar (395 m) is 25.4° C; at 1200 m, it is 20.5° C, and the lapse rate is 6° C. The Guayana Highlands are tilted upward toward the south, and this divides the Amazon from the Orinoco River watersheds. The east-central part of the Guayana Highlands is the Gran Sabana covering ~30,000 km^2, with Angel Falls (Fig. 1.42), the world's tallest waterfall, at 979 m (Niagara Falls at the United States–Canadian border is 52 m tall). A series of elegant photographs of tepuis in the Gran Sabana of the Guayana Highlands is given in Weidmann (1986). The eastern border of the Guayana Highlands slopes to the coastal plains of Guyana, Suriname, and French Guiana.

Colombia

Colombia extends from 12°24'N, the northernmost part of South America, to 4°17'S, and it is the only South American country with coasts on both the Pacific and Atlantic oceans. The town of Santa Marta was established in 1525 and is the oldest Spanish town on mainland South America. Cartagena was founded in 1533 and Bogotá in 1538.

Figure 1.41. Cerro Autana, a tepui in northwestern Amazonas, Venezuela, ~1300 m in elevation. Photograph by Charles Brewer Carias. From Steyermark et al. (1995). Used with permission of Missouri Botanical Garden, St. Louis/Timber Press, Portland, Oregon.

Figure 1.42. Angel Falls, Venezuela.

As noted previously, the Andean Mountains branch in Colombia to form the Cordillera Occidental, Cordillera Central, and Cordillera Oriental. The Cordillera Oriental includes a broad open plateau around Bogotá called the Sabana de Bogotá (Fig. 7.107). It has an average elevation of 2550 m, and there are cirque-like depressions that indicate former glaciation. Average yearly temperatures vary by ~3° C, while the daily fluctuation can be more than 20° C. This area has been the site of extensive studies by Thomas van der Hammen, Antoine Cleef, Henry Hooghiemstra, and their associates in Amsterdam and Colombia on the modern páramos and the vegetation history, paleoenvironments, and climatic processes operating in the Neotropics (Chapter 7).

The Cordillera Central is the highest in average elevation at 3040 m and includes Mount Huila (Nevado del Huila; 5750 m) and Mounts Ruíz and Tolima (5400 m). When Mount Ruíz erupted in November 1985, the melted snow created great mudflows that destroyed the town of Armero, killing nearly 50,000 people. West of the Serranía del Perijá on the Guajira Peninsula in northwestern Colombia is the granite massif called the Sierra Nevada de Santa Marta. It has an area of 7252 km^2 and is the highest coastal mountain system in the world. The highest peak in Colombia is Pico Cristóbal Colón at 5800 m, which is located in these mountains. In northwestern Colombia, there are also extensive swamps (Depresión Momposina) adjacent to the Darién of Panama, and valleys of the Cauca and Magdalena rivers between branches of the northern cordillera. The region of eastern Colombia beyond the Cordillera Oriental is known

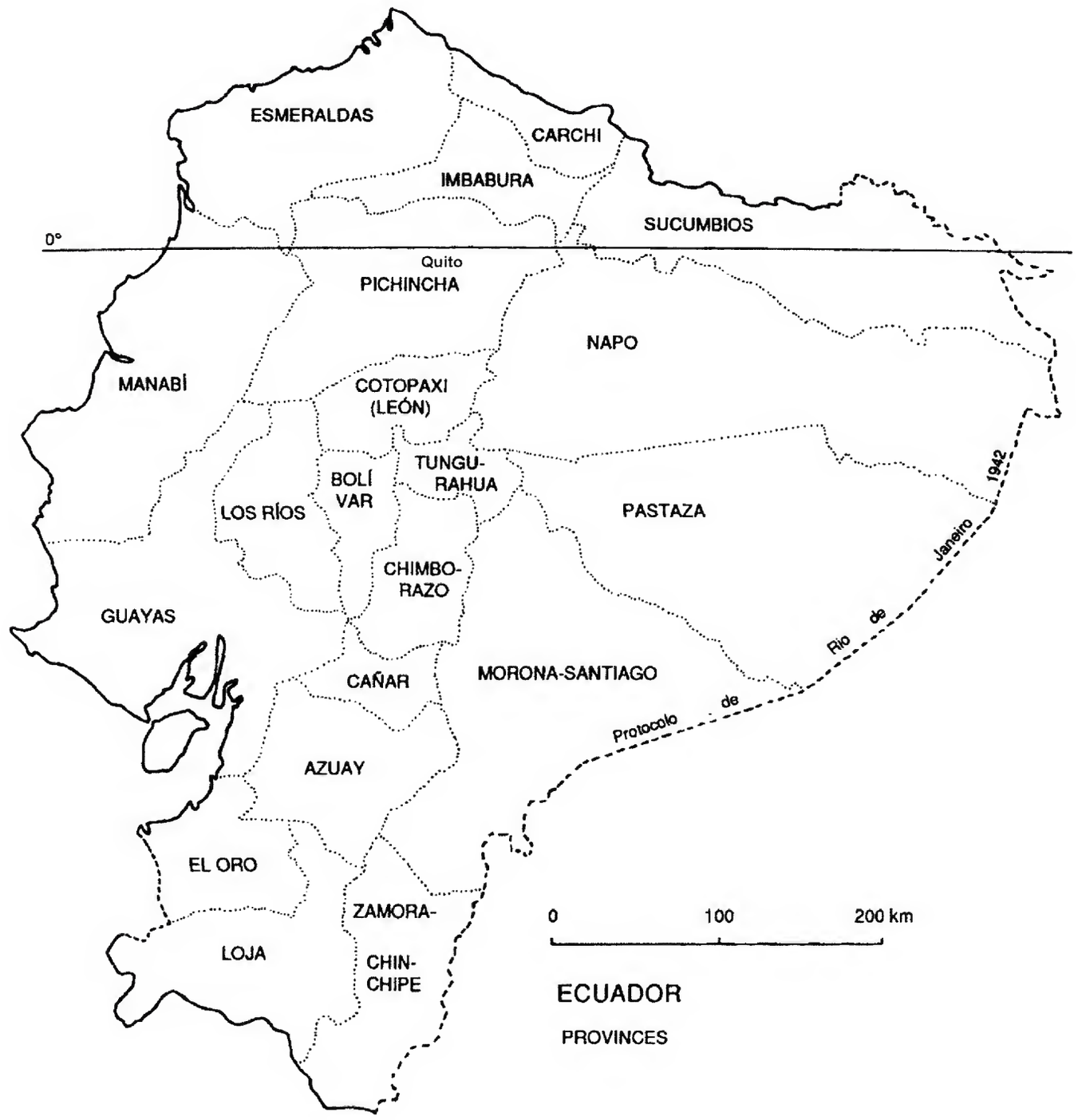


Figure 1.43. Political subdivisions of Ecuador.

as the Oriente. It is through this region that several tributaries flow to the Orinoco River including the Meta, Tomo, Vichada, and Guaviare. In southern Oriente, one of the major rivers, the Putumayo, forms the southern boundary with Peru.

At sea level, high annual temperatures range from 18.5° C in inland rainy regions to 37.8° C on the Guajira Peninsula (MAT 26° C). In Bogotá at 2618 m, the MAT is 14.5° C with an annual variation between 5° C and 24° C (lapse rate ~4.6° C/km). The snow line here is at 4877 m, and palynological studies show that it shifted significantly and repeatedly during the Quaternary period. The southwestern coast is known as the Colombian Chocó, and it is one of the wettest regions on Earth. The city of Buenaventura receives 4572 mm of annual rainfall, and greater amounts fall in the uplands. The coast is separated from the Andes Mountains by the Atrato and San Juan valleys. This isolated swampy region northward from Buenaventura (Fig. 1.34) receives nearly perpetual rain (more than 7000 mm/yr to near 11,000 mm locally), there are constant clouds, and relative humidity is greater than 85%. The land is covered by dense, very species-rich lowland tropical rain forest. Using the Chocó as one study site, Gentry (1986) showed a close relationship between precipitation and species richness. Where MAP is ~4000 mm, there are ~250 species/0.1 ha, and where it is 1000 mm or less, it falls to ~50 species/0.1 ha. One of the routes considered for the transoceanic canal was the Colombian Chocó because of its low-lying landscape and the abundant water. The Río Atrato empties into the Golfo de Urabá. This region is an important center of avian diversity and figures prominently in discussions of the refugium concept (Chapter 8). Haffer (1970) provides a good account of the geography and climate of the area. MAT is 27.3° C with a daily range of 21.4° to 30.3° C. The native inhabitants are the Cuna and Chocó Indians.

The driest region of Colombia is on the Guajira Peninsula, and it is desert and highly disturbed shrubland/chaparral–woodland–savanna. In the Cordillera Occidental, the precipitation is more or less uniform throughout the year, with a slightly wetter season between May and October corresponding to the trade wind season of March through December. A further characterization of the climates of Colombia is given by Eidt (1968) and Kuhry (1988).

Ecuador

The Spanish settlement that includes present-day Ecuador (Fig. 1.43), Peru, and Bolivia dates from 1531 when Pizarro, departing from Panama, conquered the Inca and later captured

Cuzco (1533) and Lima (1535). At the end of the wars of independence with Spain in the 1820s, a large region was established known as New Granada and later as Greater Colombia or the Colombia Confederate. Subsequently, this was subdivided into the present countries of Colombia, Venezuela, Panama (part of Colombia until 1903), and Ecuador (established in 1831). It has a land area of ~283,561 km^2 and with 12 million people is the mostly densely populated country in South America. Included as part of Ecuador are 16 islands on the equator about 950 km west of the mainland called the Archipelago de Colón or the Galápagos Islands. Colón is Spanish for Columbus, and Galápagos is the Spanish name for the large sea tortoise found on the islands. Darwin's visit to the islands was a key event in formulating his theory of evolution (Moorehead, 1969), and the Galápagos Islands are currently the site of a beleaguered biological preserve (Nature, 2004; Wikelski et al., 2001).

Mainland Ecuador consists of four physiographic provinces called the Costa (Pacific Coastal Plain to 1000 m elevation), Sierra (Andes Mountains above 1000 m), and Oriente divided into the eastern slopes of the Andes Mountains and the tropical lowlands drained by the Amazon River system. Mera in the lowlands is the site of a Quaternary spore and pollen study on refugia. The Sierra consists of the Cordillera Oriental (Cordillera Real) and the closely adjacent Cordillera Occidental. The highest peaks are Volcán Chimborazo at 6267 m and Mount Cotopaxi to the north at 5896 m with snow line at 4785 m. The mountains are crossed by dry interandean valleys that constitute barriers to the north-south migration of páramo and mid-elevation mesic organisms.

Climatic data for Ecuador are given in Naranjo (1981), Porrut (1983), and Cañadas Cruz (1983), derived from a network of meteorological stations established in the early 1960s. The location of Ecuador on the equator means that average monthly temperatures are relatively uniform throughout the year (~3° C differences or less) and change more during the day (~20° C). MAT in the lowlands is ~25° C, and the lapse rate is ~5° C/km. The principal seasonal fluctuation in climate along the equatorial Pacific coast is in rainfall, and this, in turn, involves the annual shift of the ITCZ from about 10°N (June–July) to ~2–3°S (January–December). This brings heavy rain in March–April as it moves north toward its June position, and secondarily in October as it moves south toward its December position. The overall pattern is modified locally by topography, and in southern Ecuador it is influenced by the interaction of the warm south-flowing Panama Current and the cold north-flowing Humboldt Current. The two meet at about central coastal Ecuador, and the Humboldt Current is deflected westward toward the Galápagos Islands. There is a pollen study of lake deposits on the Galápagos Islands documenting a long period of aridity, although during El Niños, warm waters flowing along southern Ecuador bring intervals of heavy rain.

Ecuador has more volcanic activity than any other country in South America, and Alexander von Humboldt, traveling through the country between 1799 and 1804, named the two cordilleras the "avenue of volcanoes." There are about 65 volcanoes of late Pliocene to Recent age, and Cotopaxi, Sangay, and Pichincha, overlooking the capital city of Quito, are particularly active. Pichincha has erupted five times since the Spanish Conquest, and in four of these eruptions the city was nearly destroyed by lava and earthquakes. The most recent eruption (mostly ash) was October–November 1999. The volcanism is due to subduction of the Nazca Plate beneath the western coast.

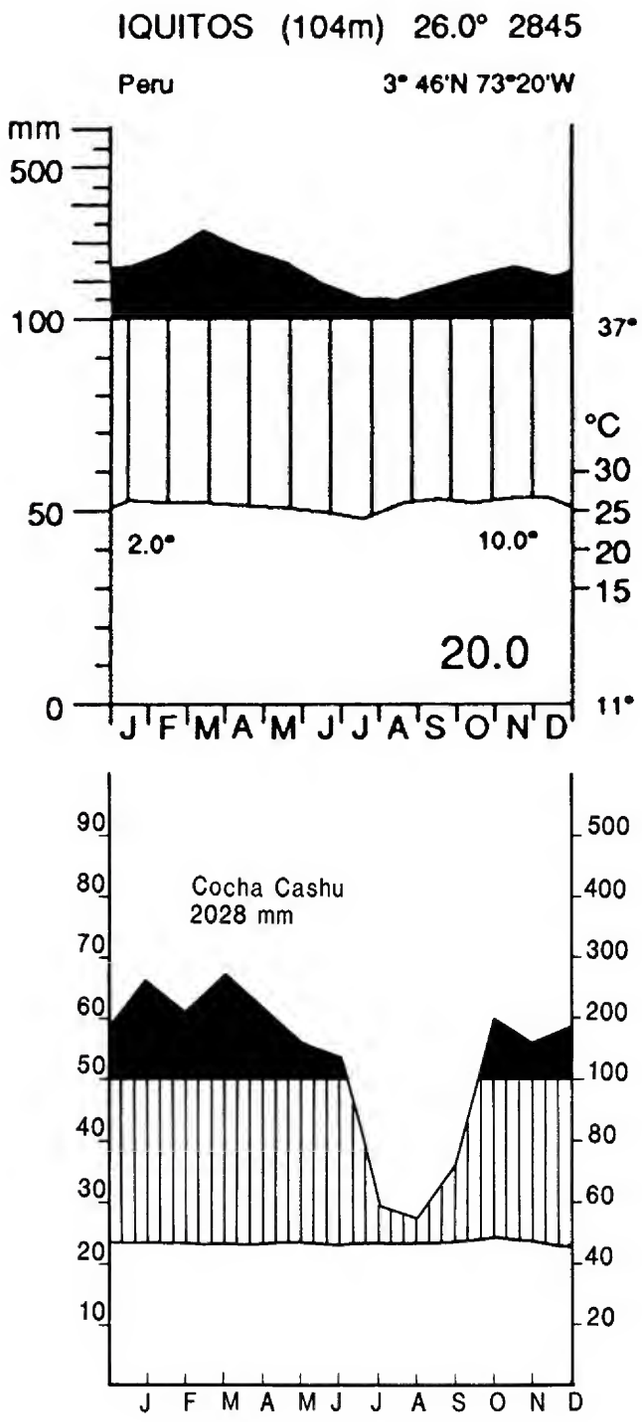


Figure 1.44. Climatogram for Iquitos and Cocha Cashu, Amazonian Peru. From Richards (1996) and Gentry (1990). Used with permission of Yale University Press, New Haven, Connecticut.

Vegetation in Ecuador is protected to varying extents in 27 national parks and preserves covering approximately 16% of the country, including the Yasuní National Park in eastern Napo (now Orellana) Province, and the Cuyabeno Wildlife Reserve in Sucumbíos (formerly Napo) Province. The Napo region is noted as a possible refugium for moist forest during dry periods of the Quaternary. Another area of interest is the Puyango Valley of Loja and El Oro provinces, where Jurassic petrified logs similar to *Araucaria* are preserved.

Peru

There are four principal physiographic zones in Peru comparable to those in Ecuador—the coastal desert, the Andes Mountains, the montaña or eastern foothills, and the Amazon Basin. The latter constitutes about 60% of the country. A climatogram for Amazonian Peru is shown in Fig. 1.44. The coastal desert in Peru is from 16 to 64 km wide, covers an area of 112,950 km^2, and extends 2240 km southward from the Golfo de Guayaquil at the Peru–Ecuador border to Arica at the border with Chile. The western edge is a steep escarpment to the Pacific Ocean, while the eastern edge merges into the foothills of the Andes Mountains. As noted previously, the desert is partly a result of winds that have lost moisture from crossing the cold Humboldt Current. The trade winds from the east also lose moisture on ascending the eastern slopes of the Andes Mountains, and upon descending the western slopes, they have an additive drying effect. Some mist (garua) in the north and streams from the mountains provide local moisture.

The area is tectonically active because the eastern edge of the Pacific Plate subducts under South America along the South American Trench. Callao was destroyed by an earthquake and tidal wave in 1746, earthquakes destroyed Arequipa in 1867 and 1868, and the associated tidal wave ruined Iquique and Arica in Chile. The highest peak in the Peruvian Andes Mountains is Huascarán at 6768 m, and in 1970 ice loosened from the western side by an earthquake killed nearly 40,000 people in the villages of Yungay and Ranrahirca. The Huallaga Valley is located between the Cordillera Central and Cordillera Oriental. This is the principal coca-growing region in South America. The Huancabamba Valley is the lowest point across the Northern Andes at 2145 m. The southern part of the Peruvian Andes Mountains is part of a high tableland in Peru–Bolivia called the Puna with elevations of 3962 to 4877 m. Plant microfossils are known from cores in Laguna Tuctua (4000 m) and Lake Consuelo (cloud forest, 1300–2000 m) in the Cordillera Oriental, and the Quelccaya ice cap is a classic site for study of Quaternary environmental history (Chapter 7).

Bolivia

> "Just over a century ago a diplomatic crisis was brewing in La Paz over a glass of chicha. The new British ambassador to Bolivia had made the mistake of sneering at this local drink when served it by the incumbent dictator. As a punishment, he was forced to drink a barrelful of chocolate and be led through the streets of the capital strapped to a donkey. When news reached London, Queen Victoria was not amused. She demanded a map of South America, drew a cross through the country and declared, 'Bolivia does not exist!'" (Alan Murphy, 1997, *Bolivia Handbook*, Footprint Handbooks, Bath, U.K.)

Bolivia is fifth in size among the 13 South American countries (~1,098,581 km^2) and, with a population of about 8.8 million people, has the second-lowest population density on the continent after the Guianas. The modern configuration of the country is a result of war with its neighbors, including the War of the Pacific with Chile (1879–1884). In that war, Bolivia's Pacific coast was lost, rendering it and Paraguay the only two landlocked countries in South America. Border disputes with Chile remain unsettled, and in the recent past some sections have been planted with land mines.

Three physiographic provinces are recognized for Bolivia—the Cordillera (Andes Mountains and Altiplano), Yungas (high slopes), and the Oriente or eastern Amazonian lowlands. The Andes Mountains are their widest (700 km) and highest (average ~4000 m) in Bolivia and consist of the Cordillera Oriental and the Cordillera Occidental (see Figs. 2.42, 2.44, 7.101). The Cordillera Oriental includes Nevado Ancohuma (Illampu) northwest of La Paz at 6550 m, Huayna Potosí (6088 m) along the Zongo Valley running north of La Paz through a subrange of the Cordillera Oriental called the Cordillera Real, and Illimani to the southwest at 6485 m at the southern end of the Cordillera Real. Sajama is to the southwest at 6542 m on the western edge of the Altiplano. Atmospheric pressure in the highlands above 5500 m is one-half that at sea level, and can make fieldwork difficult and longer-term residence by lowlanders dangerous. La Paz is the world's highest capital (3600 m), and nearby Lake Titicaca, second largest in South America after Lake Maracaibo, is the world's highest navigable lake (4000 m; MAT 8° C). Meltwaters from the Cordillera Oriental drain westward into Lake Titicaca at the border between Bolivia and Peru, and eastward via the Río Mamoré and the Río Beni into the Amazon lowlands. The lake drains about 10% of its annual water budget southward across a spillway into the Río Desaguadero that flows nearly the entire length of the Altiplano.

The Altiplano or Bolivian Plateau, comprising about 10% of the country, is a high, cold, windswept tableland that lies in the rain shadow between the Cordilleras Occidental and Oriental. It is ~800 km long, 65 to 100+ km wide, extending from southern Peru to northern Argentina, and it is the second largest and highest plateau on land with an average elevation of 3700 m. The largest and highest is the Tibetan Plateau at 4200 m (Isacks, 1988), and the largest on Earth is the submerged Ontung–Java Plateau. The MAT is 7°–10° C, with a minimum to –20° C, the MAP is 758 mm, and strong El Niños produce droughts on the Altiplano. About 70% of the population of Bolivia live either on the Altiplano in La Paz, around Lake Titicaca, or in mining towns scattered through the country.

Several megafossil floras were described from the Altiplano along the border with the Cordillera Oriental by E. W. Berry in the early 1900s near the mining towns of Corocoro, site of the world's largest deposits of copper, and the silver-rich Cerro Rico (4824 m) in Potosí. Reexamination of these and other fossil floras, together with recent data from plant microfossils, are providing new information on the uplift history of the Central Andes.

During the Pleistocene the Andes Mountains and the Altiplano of Bolivia were extensively glaciated as evident by the

ice-carved features and hummocky surfaces throughout the region. During each of the several interglacials, meltwater carved deep gorges into the mountainsides, and the last (at ~11 Kyr) left many lakes on the Altiplano including Lake Titicaca. The more shallow lakes and dry lake beds are highly saline and are called salars. The Salar de Uyuni on the Altiplano is the largest salt lake in the world (Fig. 7.101). Studies of lake levels, lake sediments, flooding patterns (e.g., along the Río Desaguadero), plant microfossils, and rodent middens are revealing the environmental history of the Bolivian Andes and the Altiplano. The region is complex, however, and the events, chronology, causes for change, and reasons for differences with other highland areas (e.g., the Northern Andes) are just being resolved (Chapter 7).

The complexity of the climate system is reflected in the description by Garreaud et al. (2003, p. 5):

> "…on all timescales, the climatic conditions on the Altiplano are closely related to the upper-air circulation, with an easterly zonal flow aloft favoring wet conditions and westerly flow causing dry conditions. Different factors influence the upper-air circulation on the different timescales. Intraseasonal variability is a reflection of the position and intensity of the Bolivian High, which is modulated by Rossby waves emanating from the mid-latitude South Pacific. The annual cycle of dry winter and wet summer conditions is caused by the seasonal expansion of the equatorial easterlies in the upper troposphere, rather than direct insolation forcing over the Altiplano or moisture changes in the source area. Interannual variability is primarily related to changes in the mean zonal flow over the Altiplano, reflecting changes in meridional baroclinicity between tropical and subtropical latitudes, which in turn is a response to sea-surface temperature changes in the tropical Pacific. Orbitally forced changes in the land-sea contrast drive continental-scale circulation changes, which significantly alter the zonal flow over the Altiplano. On glacial–interglacial timescales, the contrast in heating between Northern and Southern Hemispheres during the glacial leads to upper-air easterly anomalies throughout the tropics. On modern timescales, the marked submonthly, seasonal and interannnual changes of moisture over the Altiplano cannot be accounted for by moisture changes in the humid tropical lowlands. However, the model experiments suggest that cooler conditions during a glacial reduce moisture availability from the tropical lowlands, which counteracts the effect of the upper-level circulation, resulting in little overall change in precipitation. This observational and modeling analysis provides a physical framework for relating the mechanisms of both internal and forced climate change on the Altiplano on a wide range of timescales."

The Yungas Province descends steeply along the eastern and western slopes of the Cordillera Oriental, although Yungas is most commonly applied to the wet, forested eastern slopes of the Andes Mountains. Yungas is dry at the upper elevations and mostly rainy and heavily forested toward the lowlands. Yungas is an Aymara word meaning "warm lands." The Aymara-speaking people of the Bolivian highlands are known for the bowler-style hats worn by the women and widely used as an advertising symbol for Bolivia. They and the Quechua are both descendants of the Inca. The region has a characteristic topography consisting of folds parallel to the long axis of the mountains producing a corrugated effect (Chapter 2, Central Andes). Below are the eastern lowlands of the Oriente that constitute 70% of the country and are covered by savanna, dry forest, and lowland rain forest. The Yungas is an isolated, sparsely populated land, and it was here in 1966 that Che Guevara began his revolutionary activities in South America. He was executed in a schoolhouse in La Higuera, Bolivia, on 9 October 1967.

Southeastern Bolivia, adjacent northwestern Paraguay, and northwestern Argentina are part of an elevated region known as the Gran Chaco. It is a hot semiarid woodland for eight months of the year, but in the rainy season from December through March, it is transformed into a vast swamp.

In Bolivia, the altitudinal zones are called the puna brava (elevations above ~3800 m), puna (3800–3350 m), cabecera de valle (upper valleys; 3350–2400 m), valle (2400–1300 m), and bosque Amazónico (tropical rain forest) with campos cerrados (savannas; below 1300 m). Blouet and Blouet (1993, p. 341) provide a general description typical of the eastern slopes of the Andes Mountains from Ecuador southward to Peru and Bolivia:

> "Some of the Andean tributaries of the [Amazon] river drop more than 10,000 feet falling from the sierra to the Oriente. As a result of these deep cuts into the sierra made by the eastward-flowing streams, tropical environments extend into the mountains and exist in the valleys of incised streams. In the Andes it is often possible to follow an incised stream down thousands of feet and to move from a temperate to a tropical environment in a few hours."

A similar description is given by Lamb (2004, p. 45) for the Zongo Valley north of La Paz in the Cordillera Real of Bolivia. It descends 4000 m into the Yungas toward the Amazon lowlands. These topographies support a complex mosaic of vegetation stressed along steep altitudinal gradients. Tropical elements extend up the valleys into contact with the lower limits of the cloud forest. Relatively small changes in climate produce large changes in community composition and shifts in the position of ecotones. Basins, lakes, and bogs in these

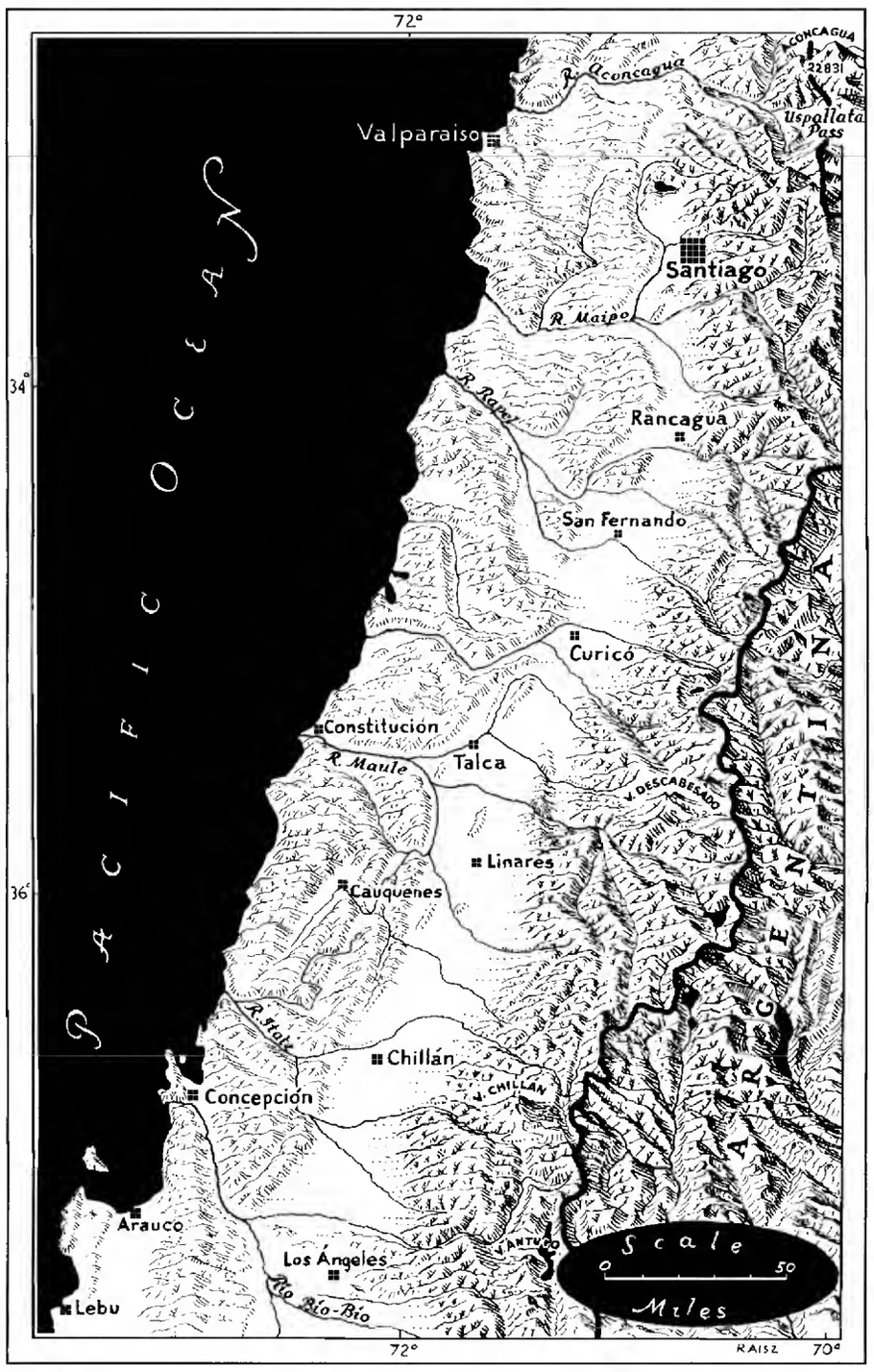


Figure 1.45. Physiographic features of central Chile. From Dallman (1998). Used with permission of Raisz Landform Maps.

vegetation and climate-sensitive regions constitute ideal sites for study of vegetational history, but progress is slow partly because travel to many parts of Bolivia is difficult. Only 4% of the roads are paved, and 80% are impassable during the rainy season from November through February. Improvements in the main road connecting Bolivia to the seaport of Arica in Chile were deliberately delayed in this military-sensitive area. It was only modernized in 1996.

Chile

The principal physiographic regions of Chile are the hyperarid Atacama Desert, extending from southern Peru (18.5°S) to Copiapó, Chile (27°S), and ~50 km inland to the Western Cordillera; the adjacent chain of low maritime mountains averaging 348 m in elevation; an agriculturally rich central valley 16 km wide and 1440 km long between the coast and the cordillera (Depresión Central); and the Andes Mountains (Fig. 1.45). The Central Valley has an average elevation of between 610 and 1220 m. The highest elevations in the Chilean Andes Mountains are in the northern and central part and include the inactive volcanoes Ojos del Salado (6893 m), Llullaillaco (6739 m), and Licancábur (5916 m) in the north, Mount Tupungato (6570 m) east of Santiago, and Maipo Volcano (5264 m) southeast of Santiago in the central part.

Northern coastal Chile is mostly dry, except in El Niño years. In the past, it was a center for nitrate mining, now mostly abandoned. South of Arica and Iquique is the mining town of Antofagasta on the Tropic of Capricorn, and northeast of there is the world's largest copper mine located at Chuquicamata near Calama. The nitrate and copper deposits, along with gypsum, reflect the arid conditions and volcanism that characterize the geologic history of the region. Many parts of the Atacama Desert are nearly devoid of vegetation (see Fig. 3.141), and the desert presents such a barren rocky landscape of salt basins (salars; e.g., Salar de Atacama, Antofagasta, northern Chile), lava flows, shifting dunes, and geysers that in June and July 1997, the NASA Ames Research Center used the site to test the robot Nomad as a prototype for lunar rovers. The robot in Chile, which could be directed by visitors to the Carnegie Science Center in Pittsburgh, Pennsylvania, traveled 200 km over a 40-day period. In an interview with the BBC, personnel at the Paranal Observatory in Chile noted that in their five-year stay, it had rained briefly three times. The biological content of Atacama soils was used to establish protocols for analyzing Martian soils retrieved by the Viking missions (Navarro-González et al., 2003).

MAP increases and MAT decreases toward the south. Santiago in central Chile receives about 355 mm of mostly austral winter rainfall per year, while the annual rainfall in southern Chile ranges from 2286 to 3556 mm. The environment between the central and southern regions is so distinct that the contact, about 480 km south of Santiago, is known as La Frontera. Across from Santiago and Valparaíso (climatogram Fig. 1.46) in the Pacific Ocean lie the Juan Fernández Islands.

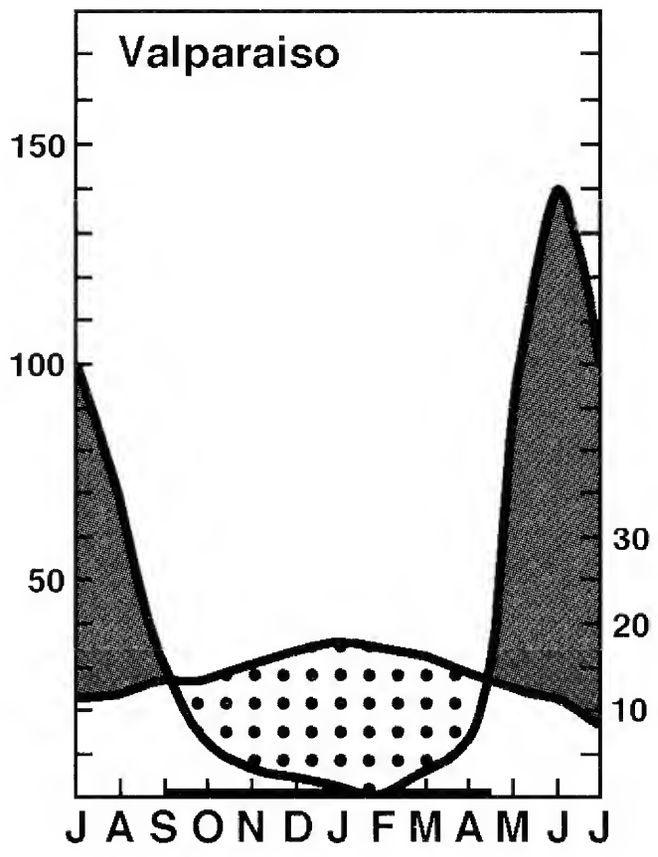


Figure 1.46. Climatogram for Valparaíso, Chile. From Dallman (1998). Used with permission of the University of California Press, Berkeley.

Figure 1.47. Puerto Montt, Chile. Photograph by J. Arthur Herrick.

On one of these islands the Scotsman Alexander Selkirk spent four years (September 1704 to February 1709) before being rescued. His life was chronicled by Daniel Defoe in the novel *Robinson Crusoe*.

The central zone between Copiapó and Puerto Montt (Fig. 1.47), dividing northern Chile with a Mediterranean climate from the cold and wet fjords of Sur Grande or Chilean Patagonia, is known as Sur Chico. It has forests of *Nothofagus* (southern beech; see Fig. 3.144) and *Araucaria* (Fig. 3.175). *Araucaria* is of interest to northern North American paleobotany because it is similar to the most abundant fossil wood (*Araucarioxylon*) in the Triassic Petrified Forest National Monument in Arizona. Southern Chile is the home of the last native population of Araucarian Indians.

The coastal mountains were formed in the late Paleozoic and Mesozoic and are lower than the Andes Mountains that were uplifted mostly in the Cenozoic. Subsidence along the South American Trench and subsequent inundation has converted the once coastal mountains south of Puerto Montt into a series of islands. The largest city in the region is Punta Arenas (Fig. 1.48) established in 1849 as a penal colony because of its isolation and its location along the shipping route from Europe through the Strait of Magellan. The importance of the city declined after the Panama Canal was completed in 1914. Inland, the Southern Andes rise to spectacular glaciated peaks and alpine plains (Fig. 1.49). The southern island of Tierra del Fuego, administered jointly with Argentina, is drenched by cold rains and has many moraines, U-shaped valleys, glaciers, bogs, and lakes. Several studies of Quaternary plant microfossils have been made in this region of South America (Chapter 7).

Figure 1.48. Punta Arenas, Chile. Photograph by J. Arthur Herrick.

Figure 1.49. Torres del Paine National Park, north-northwest of Punta Arenas, Chile. Photograph by J. Arthur Herrick.

> "I can only add raptures to the former raptures…each new valley is more beautiful than the last. It is not possible to give an adequate idea of the high feeling of wonder, admiration and devotion which fill the mind." (Charles Darwin, *Voyage of the Beagle*, and display at Down House, Downe, U.K., May 2001)

Argentina

In 1536, Pedro de Mendoza established a settlement on the Río de la Plata called Ciudad y Puerto de Santa María de los Buenos Aires. The site was soon abandoned, and the inhabitants moved 2590 km inland to the present locale of Asunción, which eventually became the capital of Paraguay (Fig. 1.34). The original site was resettled in 1580 by Don Juan de Garay who named it Ciudad de la Santísima Trinidad y Puerto de Santa María de los Buenos Aires. The city flourished as a port of entry for European explorers mostly seeking silver (the name Argentina is derived from the Latin argentium, "silver" in English and "plata" in Spanish). The cities of Mendoza and San Juan were established in 1561 and 1562, respectively, and Tucumán was founded later on the overland route between Lima and Buenos Aires. These cities were designated by the Spanish government as official ports for shipments from the colonies to Sevilla and other cities in Spain (Fig. 1.50; E. G. Ottone, pers. comm., 2005).

The Monte and the Pampas—Western Argentina borders on the Andes Mountains, which extend for 3680 km along its border. The prominent peaks are Cerro Aconcagua at 6960 m near the border with Chile, the highest in the Americas, and Nevado Ojos del Salado at 6863 m and Mt. Lanín (3740 m; Fig. 1.51) also at the Argentina–Chile border. The arid upland plains along these highlands have a climate and physical aspect similar to the Basin and Range Province of the western United States and the Central Plateau (Altiplanicie) of northern Mexico. The region is called the Monte, covering ~40 million ha between ~24° and 43°S, and it includes plants related to those found in the deserts of western North America. The area of central Argentina between 30° and 40°S latitude, and between the eastern slopes of the Andes Mountains and the Atlantic Ocean (Córdoba to Buenos Aires), includes a plain called the Pampas. It covers an area of 647,500 km^2 and is bordered on the north by the Gran Chaco and on the south by Patagonia. The name is derived from the Quechua Indian word for "flat," and it is one of the world's leading cattle-producing regions, tended by the picturesque gauchos (Fig. 1.52). It slopes down from Mendoza at 425 m in the northwest to Buenos Aires at 106 m in the southeast. The western part is dry with saline

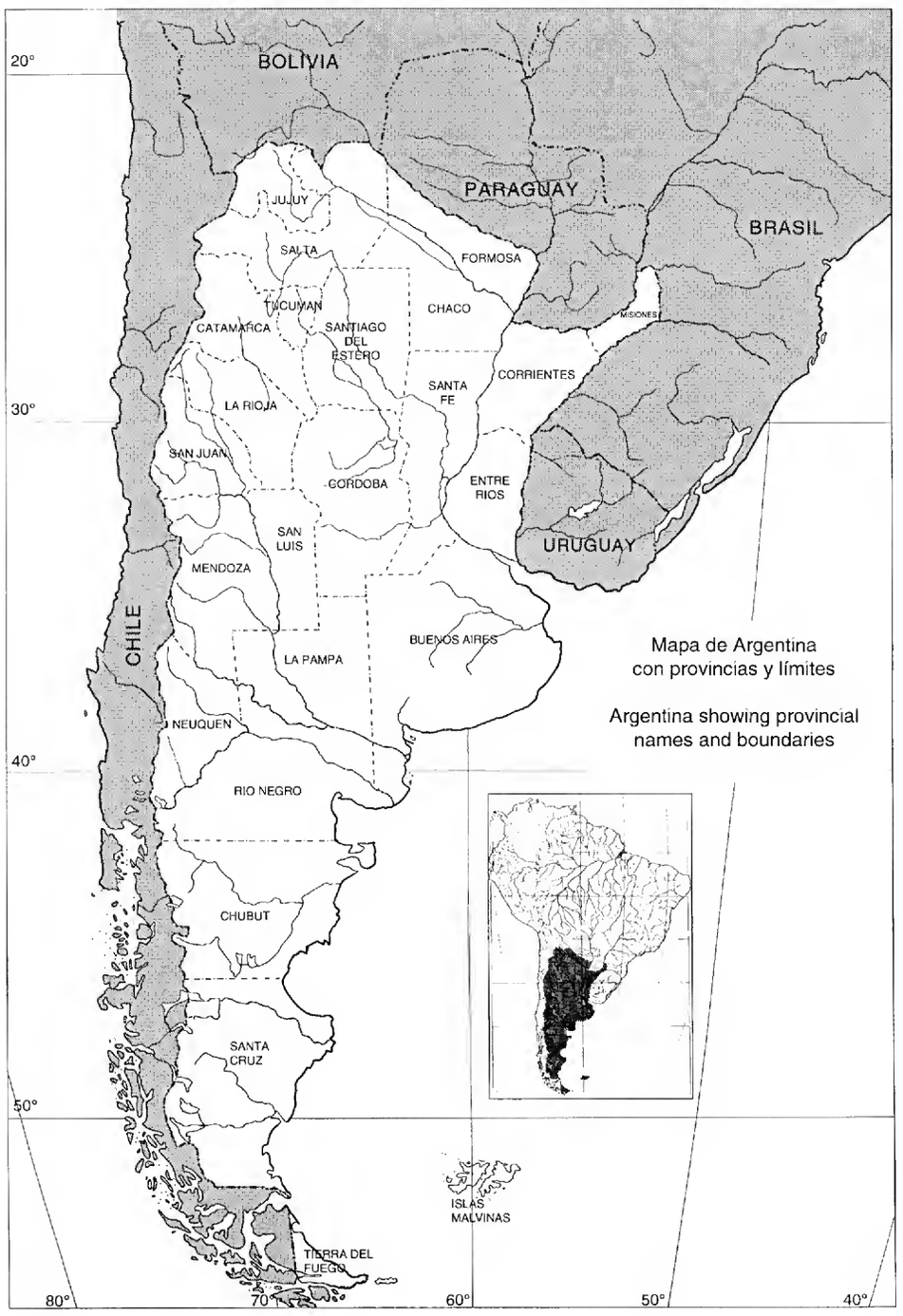


Figure 1.50. Political subdivisions of Argentina. From Zuloaga and Morrone (1999). Used with permission of the Missouri Botanical Garden, St. Louis.

Figure 1.51. Mt. Lanín, Lanín Nature Preserve, 3640 m, 39°38'S, north of Puerto Montt, Chile–Argentina border. Photograph by J. Arthur Herrick.

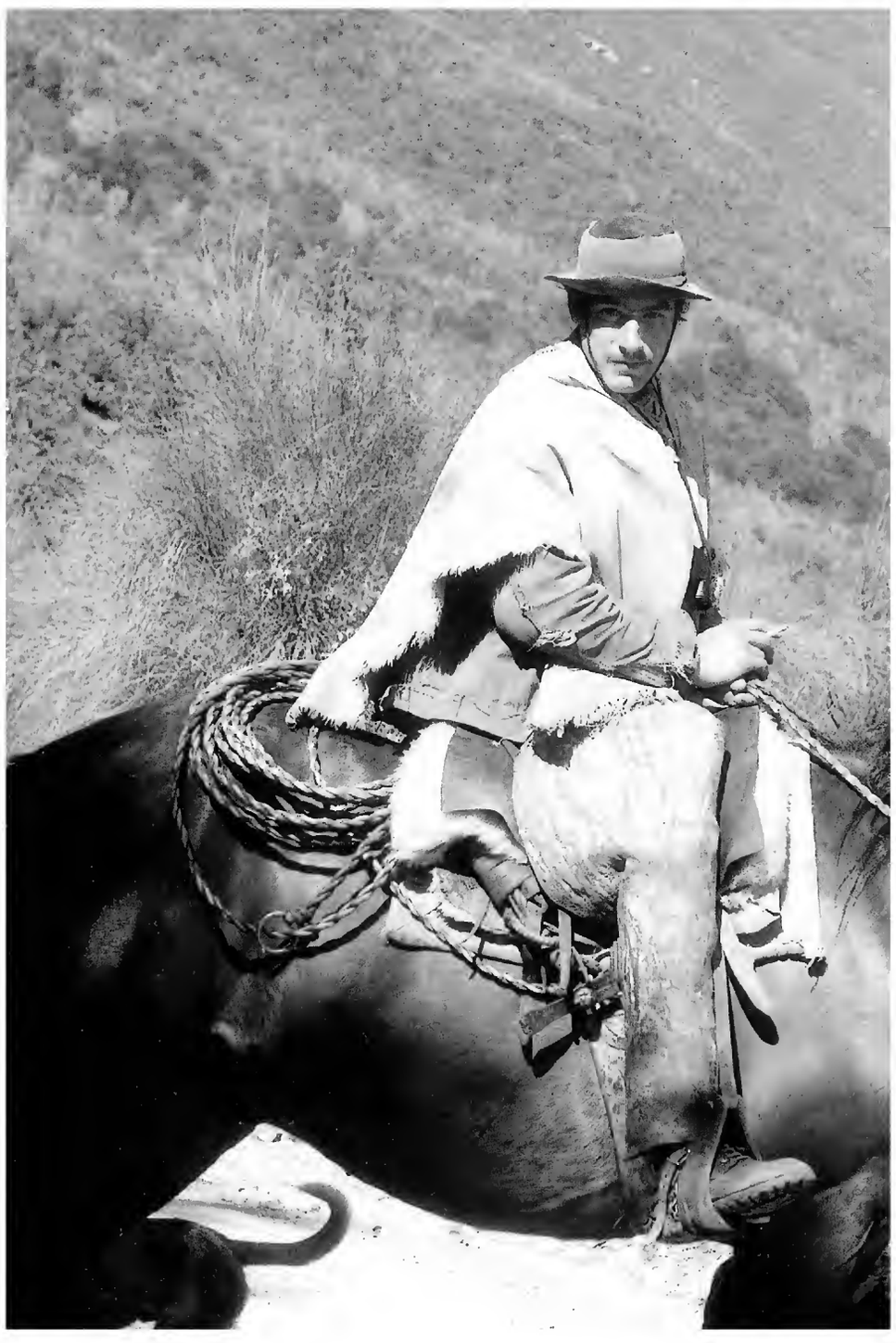


Figure 1.52. Gaucho and the Argentina Pampas. Photograph by J. Arthur Herrick.

lakes and brackish streams, while the populous eastern part is more humid (Figs. 1.53, 1.54). In central Argentina, the warmest month is January at 24°–28° C and July is the coldest at 7°–18° C. Annual rainfall is 1016 mm in the east, 508–760 mm in the central region, and drier along the western margin. A strong, cool, dusty, southwesterly summer wind meets warm air from the north to produce gales and rainstorms called pamperos, which are characteristic of the Pampas.

Gran Chaco ("the Green Hell")—Northeastern Argentina to the west of the Paraná River includes the Gran Chaco (Quechua for "hunting ground"; territories of Chaco and Formosa in Argentina, and parts of Paraguay, Bolivia, and Mato Grosso do Sul in Brazil). This extensive interior plain covers ~1 million km^2 and is bordered on the west by the Andes Mountains and on the east by the Paraguay and Paraná rivers. About half of the Gran Chaco is in Argentina, and most of the rest is in Paraguay and Bolivia. It is an arid land and supports large commercially valuable stands of *Schinopsis balansae* (known as quebracho, meaning "break-axe"), one of the hardest woods known. The logs (rollizos) are rich in tannin and extensively used for railroad ties, fence posts, and construction timbers. The climate is tropical in the north with a MAT of 25° C but reaches a maximum of 49° C and is temperate in the south where the MAT is 18° C with minima to –7.2° C. Rainfall is highest in the east (1320 mm) and decreases to 350 mm in the southwest with a hot tick-infested dry season lasting about six months. Two principal rivers flow through the Gran Chaco, the Pilcomayo and Bermejo (Teuco), which divide it into the chaco boreal, central, and austral. The largest is the chaco boreal, which covers ~259,000 km^2, and it is flat, sparsely inhabited, and covered with dry thorn woodland. It and the Pampas are part of the Paraguay–Paraná alluvial plain, which represents an ancient embayment where the Atlantic Ocean once extended inland to the Mato Grosso Plateau of Brazil.

The region between the Paraná and Uruguay rivers including the territory of Misiones and the provinces of Corrientes

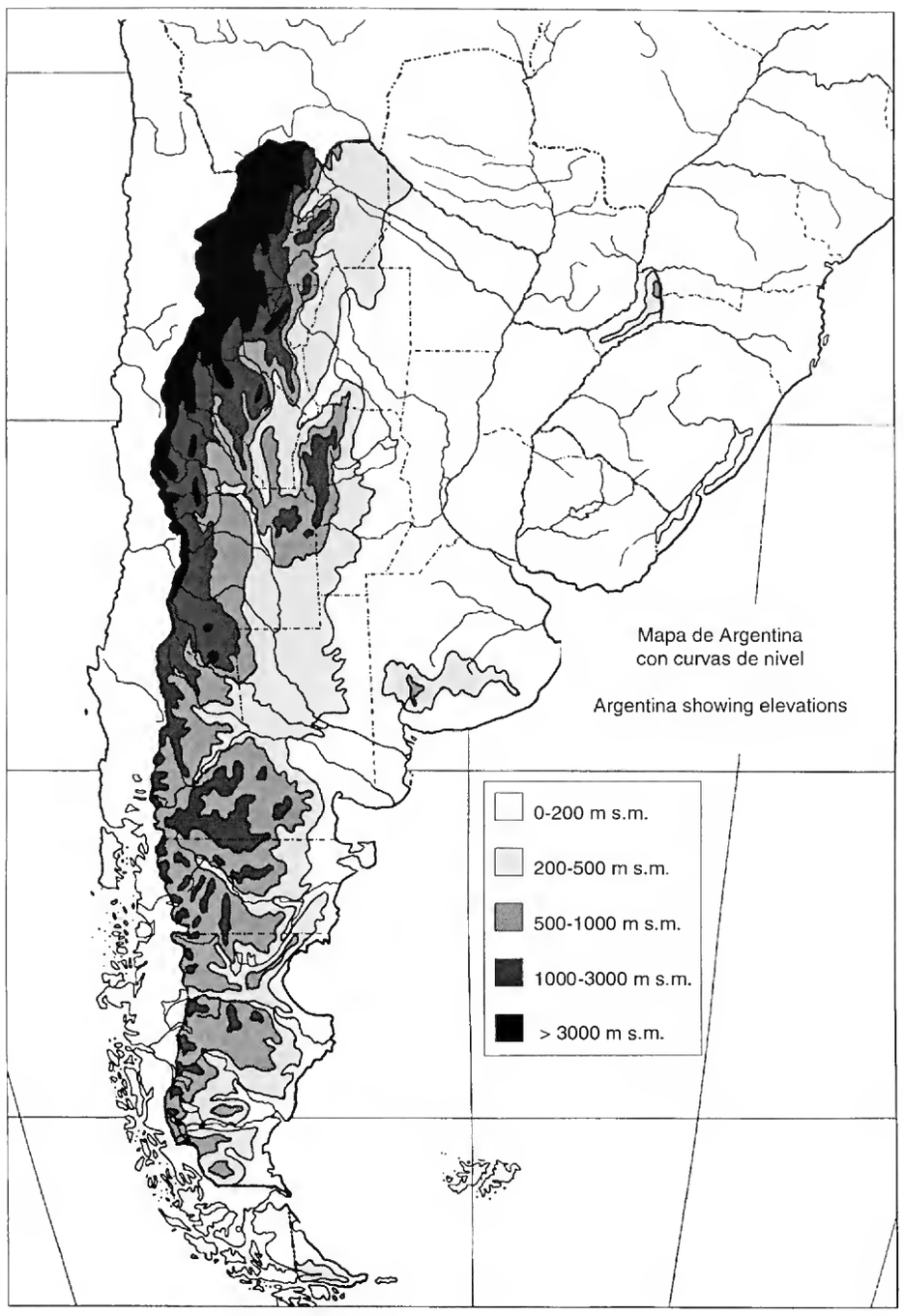


Figure 1.53. Index map of the elevations of Argentina. From Zuloaga and Morrone (1999). Used with permission of the Missouri Botanical Garden, St. Louis.

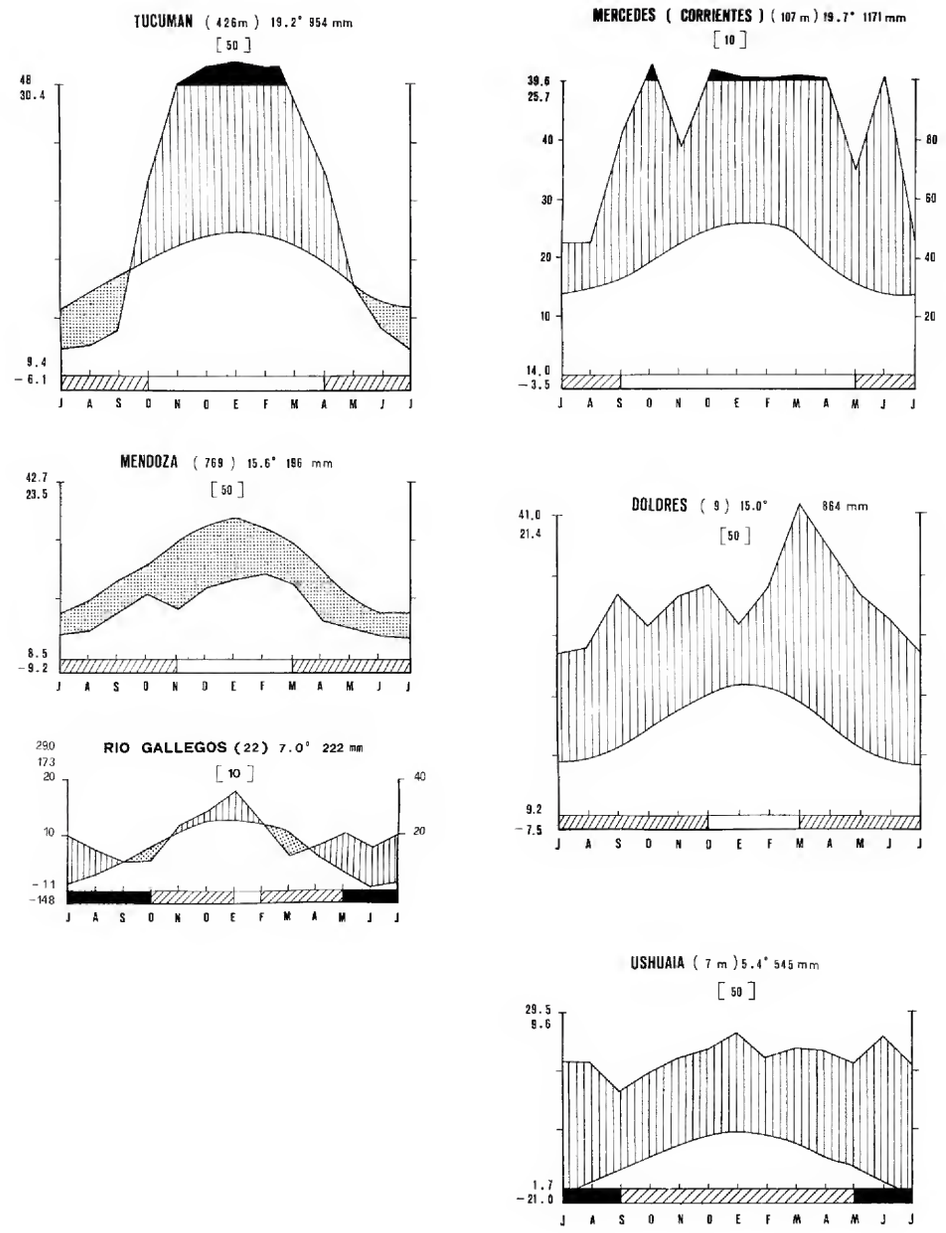


Figure 1.54. Climatograms for six sites in Argentina. From Cabrera (1976). Used with permission of Acme Agency, S.A.

and Entre Ríos ("between the rivers") is called Mesopotamia (also meaning "between the rivers"). It is a narrow depression that extends 1600 km and merges with the Pampas south of the Río de la Plata. In this area the leaves of *Ilex paraguariensis* are gathered extensively to make the stimulant drink yerba mate. Southern Argentina is called Patagonia ("The Uttermost Part of the Earth"):

> "Eventually Magellan gave the Indians a name—*Pathagoni,* a neologism suggesting the Spanish word *pathacones*, or dogs with great paws, by which he meant to call attention to their big feet, made even larger by the rough-hewn boots [patad, Portuguese for 'coarse shoe'] they wore. So these were the Bigfeet Indians, according to Magellan, who later gave the name to the whole region, known ever since as Patagonia." (From Laurence Bergreen, 2003, *Over the Edge of the World*, William Morrow, New York. p. 166)

Patagonia is south of the Pampas and comprises the provinces of Río Negro, Neuquén, Chubut, and Santa Cruz. It is in the rain shadow of the Andes Mountains and is a mostly flat, cold, and dry scrubland-desert of 900,000 km^2 with an annual rainfall of less than 254 mm. The lowest point of land in Latin America is on the Valdés Peninsula of Argentina at –13 m (Fig. 1.55). By comparison, Death Valley in southeastern California is –28 m, and lowest on Earth is the Dead Sea at –132 m. The western coast is mostly bogland, the higher western parts are moist forest (MAP 4000–7000 mm), and the eastern slopes of the Andes Mountains in Patagonia are drier (MAP 800 mm) with shrubland. The region is crossed by several rivers including the Ríos Colorado, Negro, Chubut, Deseado, Chico, Santa Cruz, Coyle, and Gallegos.

To the south of Patagonia is the Strait of Magellan, often characterized by dense fog, darkness, extreme cold, and fierce westerly winds called the Roaring Forties. The desolate aspect of the strait is vividly captured in Coleridge's *The Rime of the Ancient Mariner*:

> "The ice was here, the ice was there, the ice was all around, it crack'd and growl'd and roar'd and howl'd—like voices of a swoon." (P. H. Fry [ed.], 1999, Bedford/St. Martin's, Boston)

The first sailing across the Pacific Ocean by Europeans, in five barely seaworthy, mutinous ships, was accomplished by

the remarkable seaman Ferdinand Magellan, who sailed from Spain on 20 September 1519 with a crew of about 250 men with the goal of finding a passage at the tip of South America to the Spice Islands. The harrowing experiences of Magellan in sailing through the 334-mile strait between South America and Antarctica are symbolic of the early voyages of discovery to the New World (Boorstin, 1983, pp. 259–266, quoting Antonio Pigafetta, p. 265):

> "Wednesday, November 28, 1520, we debouched from the strait, engulfing ourselves in the Pacific Sea. We were three months and twenty days without getting any kind of fresh food. We ate biscuit, which was no longer biscuit, but powder of biscuits swarming with worms, for they had eaten the good. It stank strongly of the urine of rats. We drank yellow water that had been putrid for many days. We also ate some ox hides that covered the top of the mainyard to prevent the yard from chafing the shrouds, and which had become exceedingly hard because of the sun, rain, and wind. We left them in the sea for four or five days, and then placed them for a few moments on top of the embers, and so ate them; and often we ate sawdust from boards. Rats were sold for one-half ducado [about $1.16 in gold] apiece, and even then we could not get them. The gums of both the lower and the upper teeth of some of our men swelled, so that they could not eat under any circumstances and therefore died. Nineteen men died from that sickness, and the [Patagonian] giant together with an Indian from the country of Verzin."

One atypical bit of good fortune was that after surviving the Straits (over a period of three months and 20 days), they sailed 12,000 miles without encountering a single storm, and named the ocean the Pacific.

Many of the problems faced by the early explorers were caused by the lack of reliable maps and a means of accurately measuring longitude.[5] At the time of Magellan's voyage, the dimensions of the Pacific Ocean were underestimated by 80%.

Figure 1.55. Valdés Peninsula, Argentina. Photograph by J. Arthur Herrick.

Figure 1.56. The Beagle Channel, southern margin of Tierra del Fuego. Photograph by J. Arthur Herrick.

It is irony in the extreme that:

> "Magellan's life, just salvaged from the worst elements that nature could muster, would be forfeited by a single act of imprudence. The king of the island of Cebu, feigning conversion to Christianity, persuaded Magellan to become his ally—'to fight and burn the houses of Mactan to make the King of Mactan kiss the hands of the King of Cebu, and because he did not send him a bushel of rice and a goat as tribute.' Magellan's officers and crew begged him not to go, 'but he, like a good shepherd refused to abandon his flock.' There, on the beach of the tiny island of Mactan, on April 27, 1521, Magellan was repeatedly wounded by the poison arrows, spear thrusts, and scimitar cuts of Mactan tribal warriors.
>
> Magellan could have retreated more speedily and saved himself but he chose to cover the retirement of his men. 'When they wounded him, he turned back many times to see whether we were all in the boats. Then, seeing him dead, we wounded made the best of our way to the boats, which were already pulling away. But for him, not one of us in the boats would have been saved, for while he was fighting the rest retired.'" (Boorstin, 1983, p. 266)

Of the 250-man crew that left Spain on 20 September 1519, 18 returned on 8 September 1522.

The Strait of Magellan separates the Isla Grande de Tierra del Fuego from mainland South America. It is characterized by dense, smoke-like fog; the native people signal by fire, and they use torches to hunt birds at night. Any one of these may have given rise to the name Tierra del Fuego ("land of fire"). Three inhabitants of the island of Tierra del Fuego were subjects of a bizarre social experiment. In 1830, Captain James FitzRoy took back to England four Fuegian natives whom he named Jemmy Button, York Minster, Fuegia Basket, and Boat Memory (the latter of whom died in England). Dressed in proper British attire, they were presented to the court of King

Figure 1.57. The end of the road—Cape Horn, Argentina, the terminus of the South American continent. Photograph by J. Arthur Herrick.

William and Queen Adelaide (Moorehead, 1969, p. 49). During their three-year stay, they were taught English and indoctrinated into the Christian faith. During the voyage of the *Beagle* with Charles Darwin aboard as gentleman's companion and naturalist, the three surviving islanders were returned to Tierra del Fuego with instruction to spread the faith among the inhabitants. They quickly returned to their familiar ways, and the whole episode was as much a failure as it was presumptuous and insensitive.

The Beagle Channel (Fig. 1.56) runs along the south side of Tierra del Fuego and isolates several islands between South America and Antarctica. These islands constitute Cape Horn (Figs. 1.57, 1.58), named by Dutch sailors for their home port of Hoorn, and they are the southern terminus of the South American continent.

Guyana

The South American countries beyond the Andes Mountains are Guyana (British Guyana), Suriname (Netherlands Guiana), French Guiana (Guyane Française, a dependent of France), collectively the Guianas[9]; and Brazil, Paraguay, and Uruguay. The region of the Guianas is coastal plain formed partly by Precambrian sediments eroded off the Brazilian Shield by the Amazon River and swept westward by the North Equatorial Current. It is mostly hot and humid lowlands with little seasonal variation (less than 2.6° C at Georgetown, Guyana). Rainfall is usually in excess of 2230 mm annually, and it is uniformly distributed with only a slight dry season between September and November.

Much of coastal Guyana is developed because of earlier occupation by the Dutch who built a system of seawalls, floodgates, dikes, and canals. The cover of Quaternary alluvial and peaty soils has retained its fertility through long periods of cultivation, in contrast to the lateritic soils of the interior. The main population centers are the ports of Georgetown and New Amsterdam located where the Mazaruni, Demerara, and Berbice rivers flow into the Caribbean Sea. Inland from the coastal alluvial sediments is Precambrian bedrock, which forms the Kaieteurian Plateau and Kaieteur Falls with a height of 225 m. The plateau is sandstone and shale and supports a grass and shrub vegetation called the Rupununi Savanna growing on leached white sand. Plant microfossils are known from the Jurassic–Cretaceous of the savanna and from well cores in the Paleocene–Eocene along the coast. South of the plateau are the Pakaraima Mountains at the border between Venezuela and Brazil. The highest point is Mount Roraima at 2743 m. The highlands in the region of southwestern Guyana, eastern Venezuela, and adjacent Brazil are called La Gran Sabana.

Suriname

Suriname is the second largest of the Guianas and, like Guyana, the coastal area is formed by sediments of the Amazon River. The coast is developed commercially, protected from flooding, and is the most densely populated part of the country. The coast was originally swamp with peaty soil that was reclaimed by the Dutch to form the New Coastal Plain. Behind the coast is a region of rolling hills known as Zanderij. The southern 80% of the country is more mountainous (Wilhelmina Mountains with Juliana Top at 1230 m) and

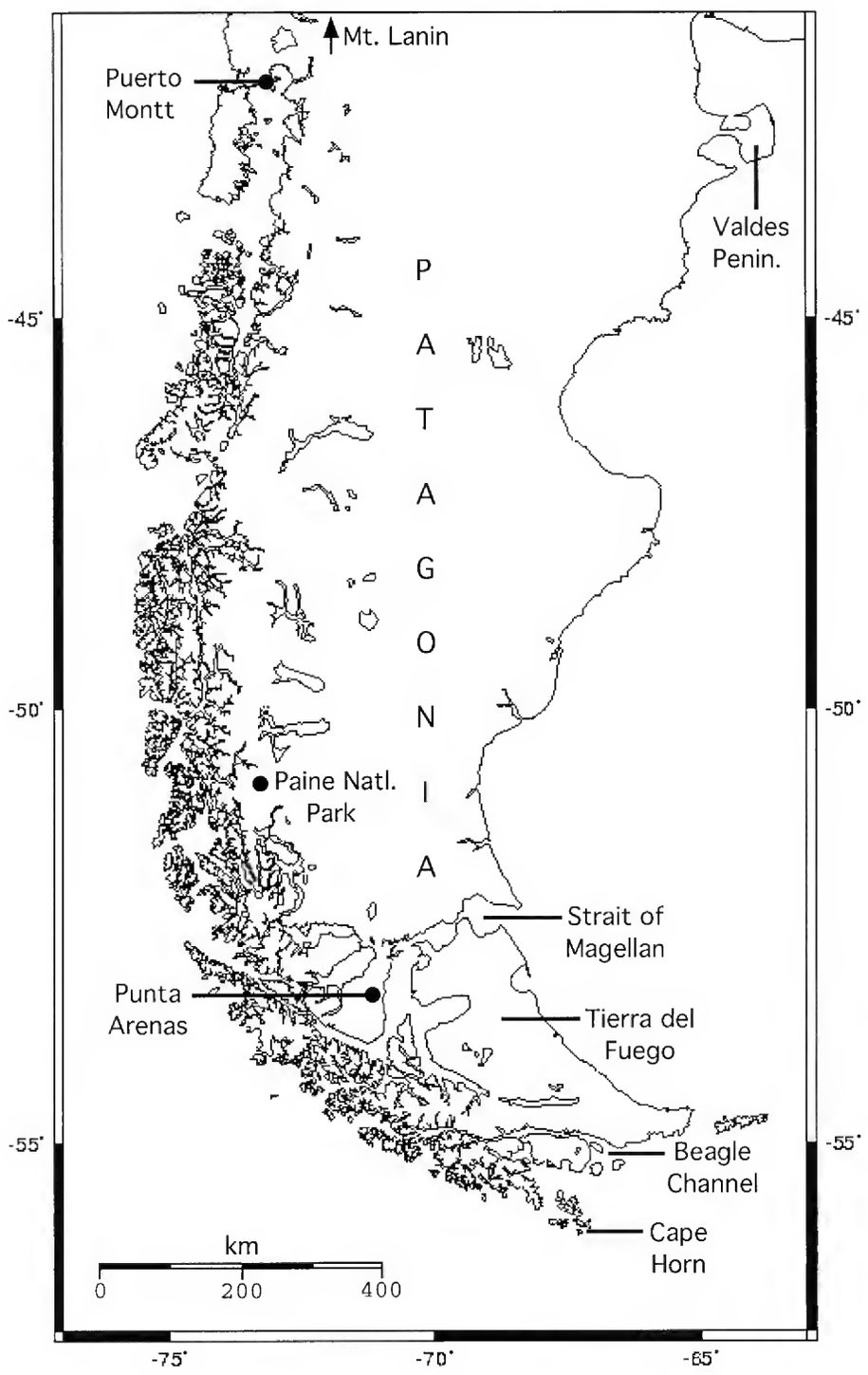


Figure 1.58. Index map of southern South America showing place names mentioned in the text. Base map modified from www.aquarius.geomar.de.

mostly covered by tropical rain forest. The principal river is the Suriname River, and the port capital of Paramaribo is located where the river empties into the Caribbean Sea.

French Guiana

The coastal plain of French Guiana is higher than in the other two colonies, and the elaborate system of drainage and flood control is not needed. The Litani and Maroni rivers form the western border with Suriname and the Oyapock River flows along the boundary with Brazil. The only highlands are the Serra Tumucumaque in the south at 690 m. Eighty percent of the country lies south of the coastal plain and is covered by tropical forest. The capital of Cayenne is located on a sandstone promontory slightly elevated above the coastal plain, and there the climate is hot and wet. Annual rainfall at Cayenne is 3200 mm and the MAT is 27° C. French Guiana is probably the best situated of the Guianas, but it was neglected by the French and there has been little development. In earlier years, French Guiana was known for Devil's Island, an offshore prison housing France's most dangerous criminals. Transport of French prisoners to the island ceased in 1938, and the last left in 1953.

Paraguay

Juan de Ayolas began the European settlement of Paraguay at Asunción in 1537. Because of its turbulent history, the country has been called the land of many misfortunes:

> "At the time of independence in 1811 Paraguay was apparently ready to become a progressive nation. Its territory was large, covered thickly with plantations and cattle ranches. In the middle of the past century a "strong man," Carlos Antonio López, became the first constitutional president. At his death, Paraguay was rich, populous, and progressive—one of the most progressive nations on the continent at the time. His son was a headstrong, foolish tyrant who dreamed of becoming a South American Napoleon. When Francisco Solano López, the son of the able dictator, attempted to create his empire in the heart of South America with Paraguay as the center, he brought upon his country war with Brazil, Argentina, and Uruguay, a triple alliance. His army was strong and he was an able general, but the other nations overwhelmed him with men. As a result of this bitter and devastating conflict, which lasted five years, from 1864 to 1870, Paraguay was almost annihilated. It was compelled to cede 56,000 square miles of territory to its adversaries. Nearly the entire male population was destroyed, and many of the women and children died of pestilence or starvation. From a prosperous nation of a million inhabitants, Paraguay was reduced to a ragged and hungry few hundred thousand." (Carlson, 1952, p. 197)

Figure 1.59. Political subdivisions of Brazil.

The country is roughly divided north and south by the Río Paraguay into the Chaco Boreal of 246,000 km^2, and the Región Oriente of 159,000 km^2, with broad lowlands of ~230 m elevation on either side. The vegetation is mostly thorny tropical dry forest of cacti, *Schinopsis lorentzii* (quebracho), *Ilex paraguariensis* (yerba), and a characteristic lowland fan palm *Trithrinax brasiliensis* (carandai). The Región Oriente is an extension of the Mato Grosso Plateau and ranges in elevation from 50 to 762 m. The highest point in Paraguay is Mount San Rafael at 850 m in the Cordillera San Rafael in the southeastern part of the country. The Chaco Boreal covers an area of 246,827 km^2, and it is named to distinguish this part from the Gran Chaco of Argentina. The MAT is 22°–24° C and annual rainfall is 1371 mm. There is local freezing in the winter, while temperatures in the summer rise above 37.8° C with dry hot winds.

Uruguay

The physiographic features of Uruguay represent the southern terminus of the Brazilian Highlands, and its vegetation is similar to that of the Argentine Pampas. About 70% of the country is now pasture. It has a relatively uniform topography of undulating uplands mostly below 520 m and low rolling hills that make up 75% of the country. Drainage is either into the Río Uruguay, Río de la Plata (named for deposits of silver anticipated by Spanish explorers), or Lagoa Mirim. The Río Paraná is 3200 km long and empties into the ocean near the southwest corner of the country adjacent to Buenos Aires, Argentina. The Río Paraguay is 2400 km long and flows along the western border. Both temperature and rainfall are moderate, and there is no pronounced seasonal variation.

Brazil

The earliest Portuguese settlements in Brazil date from 1500–1530. They were mostly small coastal centers based on the harvesting of *Caesalpinia echinata* (pau-brasil) for its purple dye used in textiles, and later for making fine bows for stringed instruments (Rymer, 2004).

Northwestern Brazil (states of Amazonas, Pará, Roraima, Amapá, Acre, Rondônia; Fig. 1.59)—

> "The first of these expeditions was the strange adventure of Don Francisco de Orellana. Orellana departed from Quito…in February 1541 as a member of an expedition led by Gonçalo Pizarro in search of cinnamon and of the land of 'El Dorado', the legendary golden kingdom. When the expedition ran out of food, the situation became perilous, and Pizarro and Orellana decided to separate. Driven by famine, the latter continued with his men in an eastern direction in search of food. Finally, no longer able to proceed on land, he ordered that a boat be built…at the confluence of the 'Rio de los Omáguas,' now the Rio Napo, with the Rio Aguárico. By the end of 1541, he had embarked in it, together with 55 Spanish soldiers and two Fratres, one of whom, Frey Gaspar de Carvajal, became the chronicler of the voyage. Instead of finding either El Dorado or cinnamon, Orellana discovered the mightiest river on earth, the 'Rio de las Amazonas,' first given the name 'Rio de Orellana.' The boat followed the current of the river down into the unknown until it came out at the mouth into the Atlantic on August 26, 1542.
>
> Only a few sections of Father Carvajal's report are interesting from a natural Sciences' standpoint. One of the most worthwhile is the paragraph, 'On the same day…we saw the mouth of another big river, on the left side, which entered that one in which we navigated, and of water as black as ink, and therefore we gave it the name of Rio Negro.' In these laconic words the greatest tropical blackwater river was made known for the first time in history to European civilization." (From Sioli, 1984, pp. 1–2; Fig. 1.60)

Figure 1.60. Confluence of the white water Rio Solimões with the black water Rio Negro below Manaus. From Sioli (1984). Used with permission of Dr. W. Junk Publishers, Dordrecht, The Netherlands.

One of the many popular misconceptions about Amazonia is that is it has a uniform topography supporting a continuous vegetation of tropical rain forest. Although the relief is generally less than 300 m and rain forest is the principal vegetation, there is considerable local variation. In addition to rain forest and the different communities occupying lake and river margins, as well as inundated versus terra firme habitats (normally beyond the influence of floods), there are others resulting from edaphic and topographic differences that support grassland-savanna and dry forest on promontories and on sandy soils (Dickinson, 1987). Even within the terra firme forest there is a level of diversity that has not been widely recognized (Tuomisto et al., 1995). The mosaic nature of the vegetation has figured prominently in models of past environmental and biotic history proposed to explain the unexcelled biodiversity (Chapter 8, Refugia). In the broadest definition, the Amazon Basin and the surrounding borderlands cover 6 million km^2, and it is traversed by a labyrinth of rivers on which small ocean-going boats can navigate 10,000 miles of water and those with a draft of two feet or less can move across 100,000 miles of waterway. The Amazon River is 6450 km long and forms the largest of all drainage systems at 7,050,000 km^2. Tributaries originate mostly in the Andes Mountains of Ecuador (Río Napo) and Peru (Río Ucayali) and in the Guayana Highlands. An estimated 160,000,000 tons of silt are transported by the waters each year, and during floods the river may rise locally up to 10 m, inundating the adjacent floodplain called várzea. Tributaries flowing into the Amazon are broadly characterized as black water and white water rivers (Fig. 1.60). Those that flow into the lower reaches from the north across the eroded, sediment-sparse Precambrian shield enter the Amazon as mineral-poor and organic-rich "black waters." Tributaries from the west into the upper reaches of the Amazon River drain the Andes Mountains and are mineral-rich "white waters."

Large sections of land or terras cahidas ("fallen lands") may become detached along its course to create furos (small bays).

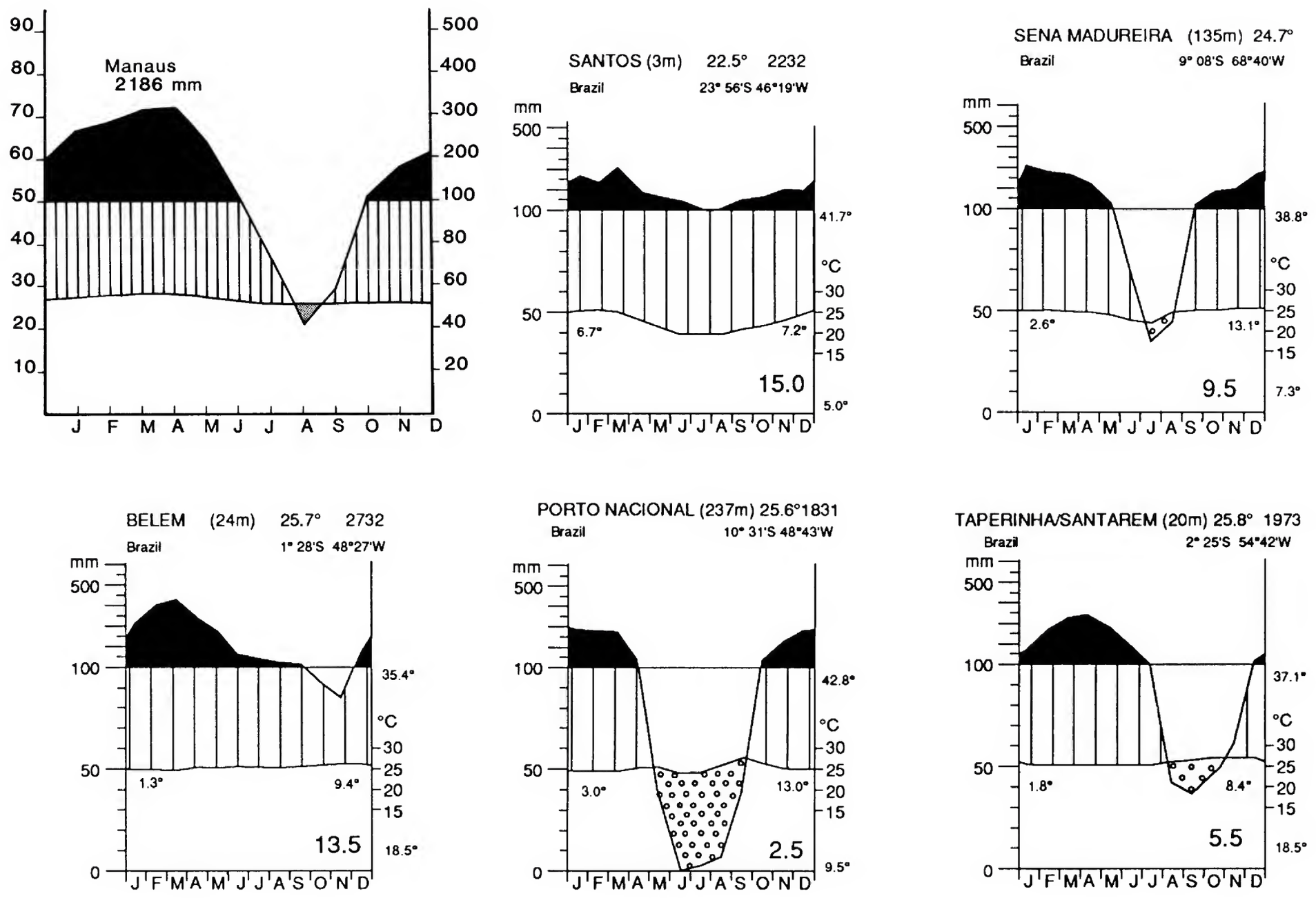


Figure 1.61. Walter climatograms for Manaus (Gentry, 1990) and other sites in Brazil (Richards, 1996). Used with permission of Yale University Press, New Haven, Connecticut.

There are thousands of these bays, lakes, and lagoons throughout Amazonia. The length of the river and the seasonality of rainfall cause flooding first in Peru during January, in April in the middle section, and in June near the Atlantic Ocean. After flooding, it takes about four months for the waters to recede. The shallow channel allows tides to reach 650 km upstream with fluctuations in water level of 1.5 m. The meeting of the onrushing sea water with the river water is called the pororoca, the tidal inflow can reach 10–15 mi/hr, and it produces waves 3–6 m in height.

In most of the low-lying areas of Brazil, temperatures may be 32° C during the day and 15° C at night, while the annual average variation at coastal Belém and at inland Manaus (Fig. 1.61) is from 25° C in September to 26.7° C in July. The highest peak in Brazil is Pico da Neblina at 3014 m in the northwest at the Venezuela border.

Northeastern Brazil (states of Bahia, Sergipe, Alagoas, Pernambuco, Paraíba, Rio Grande do Norte, Ceará, Piauí, Maranhão, Tocantins, and the island territory of Fernando de Noronha)—Most of eastern Brazil is an ancient Precambrian crystalline structure known as the Brazilian Shield or the Brazilian Highlands that separates the Amazon forest from the Atlantic forest. The highest elevation is in the Chapada Diamantina at Esbarrancado (1700 m). It continues southward as the Serra da Mantiqueira and the Serra do Mar. The east-facing portion of the Brazilian Highlands is known as the Great Escarpment, which, around Rio de Janeiro, drops 1000 m to the ocean. The Rio Paraná flows across the southern part of the shield and descends at Iguaçu Falls into the lowlands of Entre Ríos, the land between the Paraná and Uruguay rivers of Uruguay and northeastern Argentina. The combined falls are 2700 m wide and 72 m high, compared to Niagara Falls, which are 1600 m wide and 50 m high. The highlands include some of the driest parts of Brazil, with an annual rainfall of less than 500 mm in many places, a pronounced dry season, and frequent droughts. Interior Ceará received no recorded rainfall between 1928 and 1931, and in the early years of the 20th century it was considered one of the major famine areas of the world.

To the far northeast is the Borborema Plateau with an elevation of between 457 and 914 m. One of the principal rivers in northeastern Brazil is the São Francisco, which flows through the center of the Brazilian Highlands at an elevation of 300–400 m with flanks on either side of about 1600 m. The valley of the river covers 595,700 km^2, and the Paulo Afonso Falls are estimated to be potentially capable of providing 10%

Figure 1.62. Geographic location of the Pantanal. From Swarts (2000). Used with permission of Waterland Research Institute, Gouldsboro, Pennsylvania.

or more of Brazil's total hydroelectric power. MAT is 27° C (18° C in the winter months), and MAP in the upper São Francisco River Valley is between 763 and 1506 mm (400 and 800 mm along the drier sections). In the densely forested coastal or mata zone, it is 2030 mm. Spores and pollen from local bogs indicate that it was very dry during phases of the Quaternary, as also reflected by paleodunes currently stabilized by caatinga and cerrado vegetation.

East-central Brazil (states of Minas Gerais, São Paulo, Rio de Janeiro, Espírito Santo)—In this region, there is a narrow coastal plain with the huge population centers of Rio de Janeiro and São Paulo, and the smaller but still large centers of Curitiba and Porto Alegre to the south. Inland from the coastal plain in the vicinity of Rio de Janeiro and São Paulo is the Serra do Mar with elevations to 2042 m. To the north is the Serra da Mantiqueira, which includes the highest peak fully in Brazil—Pico da Bandeira at 2890 m. This range continues north beyond Belo Horizonte as the Serra do Espinhaço, with Pico do Itambé near Diamantina the highest point at 2033 m. To the south, a natural break occurs in the Serra da Mantiqueira called the São Paulo Basin where the city of São Paulo is located. The average summer temperature here is 23° C and the winter temperature averages 18° C. Farther inland on the lower slopes of the highlands, temperatures reach 35° C in the summer and 14°–18° C in the winter. At higher elevations, frost may occur but there is no snow. Annual precipitation in the coastal lowlands is 1524 mm, and it increases to a maximum of 3302 mm on the adjacent slopes where the vegetation is tropical forest. Maximum precipitation occurs during the austral summer months of December through February. Higher on the slopes above the zone of maximum precipitation, annual rainfall decreases to 1016 mm and the vegetation is savanna.

West-central Brazil (states of Goiás, Mato Grosso, and Mato Grosso do Sul, Distrito Federal)—This region includes the southern part of the Amazon Basin and its extensive river system of the Rios Tocantins, Tapajós, Amazonas, and Negro. Two major physiographic features are the Goiás Plateau, a dissected and rolling peneplain of ancient basement crystalline rocks along the east-central margin of the Brazilian Highlands, and the flatter Mato Grosso Plateau composed of sedimentary rocks. The Rio Tocantins, flowing into the Amazon, and the Rio Alto Paraná drain the area of the Goiás Plateau. The Mato Grosso Plateau includes parts of the states of Mato Grosso, Amazonas, Pará, Goiás, and Maranhão. The northern part has heavy rainfall and forest vegetation. The southern part is drier and has savanna on the high flat tableland (chapada) that supports much of the vast soybean and cattle industry of Brazil. One section of the plateau west of Cuiabá is the Planalto do Mato Grosso. It is 480 km across with linear extensions toward the north between which flow streams that become major tributaries to the Amazon River.

Pantanal (Figs. 1.62, 3.150)—To the southwest of the Mato Grosso Plateau, beginning at about Cuiabá, there is a low northerly extension of the Gran Chaco situated between latitudes 16° and 22°S along the border of Brazil (Mato Grosso–Mato Grosso do Sul) with Bolivia and Paraguay. It is called the Pantanal (meaning "great swamp" in Portuguese) and consists of an extensive alluvial plain with a vast network of rivers and raised ancient deltas with numerous lakes. The Paraguay River floods during the rainy season of October through March, rising more than 5 m and leaving only hills emerging above a vast sheet of water. The Pantanal is the world's largest wetland system, covering an area of 140,000–170,000 km^2, or 15 times greater than the existing Florida Everglades (Por, 1995; Pott & Pott, 1997; Heckman, 1998; Swarts, 2000; Gottgens, 2001). MAP is 1600 mm in the highlands to the north (600 m) and 800 mm at lower elevations (90 m) to the south.

This complex hydrological system performs critical functions such as flood abatement and water filtration and provides habitats for an estimated 656 species of birds, 263 species of fish, 162 species of reptiles (including a caiman [*Caiman yacare*] population estimated at 10 million individuals), and 95 species of mammals (46 of which are rare or endangered). These are minimal figures and the region is regarded as a "mother lode of unrecorded life" (Swarts, 2000). However, 98% of the land is privately owned, and there is a proposal for a navigable waterway (the Hidrovia) 3440 km long to develop agriculture, ranching, mining (diamonds, gold, iron, manganese), and ecotourism (Gottgens et al., 2001; Junk & Nunes de Cunha, 2005). It is also an area with "woefully inadequate health services, poor schools, inferior communications and transport, and lack of employment opportunities" for the Pantaneiros (Swarts, 2000). The Pantanal has already been the subject of

two international conferences to discuss the multifaceted and immensely complicated issues of conservation and sustainable development of the region.

Southern Brazil (states of Paraná, Santa Catarina, and Rio Grande do Sul)—This region consists mostly of an upland dissected plain that is an extension of the Goiás Plateau–Brazilian Highlands. The annual rainfall is 1524 mm, and the average elevation is 610 m with some peaks of 1524 m. The vegetation is tropical forest in the northeast, more open forest in the northwest, and savanna and open grassy fields in the south (campos do sul). The region is bordered on the southeast by a narrow coastal plain along which is located the city of Porto Alegre and the lagoons of Lagoa dos Patos, Mirim, and Mangueira.[10]

An increasing number of fossil plants are being reported from Brazil, including gymnosperm and angiosperm megafossils of Cretaceous and Paleogene age (Table 7.1), as well as others from the Neogene (Table 7.2), and the Quaternary (Table 7.6).

This brief characterization of the physical geography of Latin America provides reference points for the principal geologic features, identifies the landscape and broad environmental conditions under which the present vegetation exists, and introduces the distribution and location of the principal fossil floras. When landscapes change, this constitutes a forcing mechanism for alterations in the composition, distribution, and evolutionary processes in the plant and animal assemblages. The landscapes of Latin America have changed dramatically through Late Cretaceous and Cenozoic times, and this history is summarized in the next chapter on the geology of Latin America.

NOTES

1. Among the several organizations defining Latin America are the Pan American Union (known since 1948 as the Organization of American States, OAS), Caribbean/Central American Action (C/CAA, related to a U.S. legislative concept called the Caribbean Basin Initiative), Latin American Integration Association, and the North American Free Trade Agreement (NAFTA).

2. The wettest 12 months ever recorded occurred in Cherrapunji, northeastern India (annual average rainfall 11,420 mm), where 26,470 mm (1040 in) fell between August 1980 and 1981. Cherrapunji also holds the record for most rainfall in a single month at 2930 mm (115 in) in July 1961, and Cilaos on Réunion in the Indian Ocean received a 24-hour record 1870 mm (73.6 in) of rain on 15–16 March 1952.

3. On 27 March 2000 at about noon, strong winds suddenly swept down from the Baja California mountains, causing huge waves in the Gulf of California. A research group was returning from fieldwork on the Isla de Cabeza de Caballo about 6 km offshore from the fishing village of Bahia del Los Angeles. The tragic result was the deaths of Gary Polis, chairman of the Department of Environmental Science and Policy at the University of California at Davis; Michael Rose, a postgraduate student at Davis; and Takuya Abe, Masahiko Higashi, and Shigeru Nakano of Kyoto University, Japan. (Accounts of the accident appeared in *Nature*, 6 April 2000; *Science*, 7 April 2000; and in an Associated Press news story for Thursday, 30 March 2000.)

4. The Web site of the Organization of Biological Field Stations (OBFS) at http://www.obfs.org maintains a partial list of field stations in Latin America. See also, "The Effectiveness of Parks" (http://www.sciencemag.org/cgi/content/full/293/5532/1007a).

5. See Dava Sobel and W. J. H. Andrews, 1998, *The Illustrated Longitude*, *The True Story of a Lone Genius Who Solved the Greatest Scientific Problem of His Time*, Walker and Company, New York. The film version of John Harrison's building of a clock that kept precise time at sea, thus permitting the first accurate measurement of longitude, is A&E's *Longitude*. The invention opened the way for the great era of Spanish-Portuguese voyages of discovery in the 18th century. See also J. D. Fernie, 2002, Finding out the longitude. Amer. Scientist 90: 412–414, and Jonathan Betts, *Time Restored: The Harrison Timekeepers and R. T. Gould, the Man Who Knew (Almost) Everything*, Oxford University Press, Oxford, U.K. (review in *Nature* 444: 821).

6. The world ranking of ocean depths along the ocean trenches are the Mariana Trench (11,022 m), Tonga (10,882 m), Japan (10,554 m), Kuril (10,542 m), Mindanao (10,497 m), Kermadec (10,047 m), Puerto Rico (9220 m), New Guinea (9140 m), Peru–Chile (8050 m), and Aleutian (7822 m). The greatest depth in the Middle American Trench is 6662 m.

7. Use of the British administrative terms "Leeward" and "Windward" islands is confusing because the Leewards are not to the lee (west) of the Windwards but north. Also, the original Spanish usage (Windwards = Lesser Antilles; Leewards = islands off the north coast of South America) is not the same as later Dutch usage (Leewards = the ABC islands; Windwards = other Dutch territories in the Caribbean region).

8. Balboa had befriended Comacho, cacique (leader) of the Indians, who reciprocated with a gift of 4000 ounces of gold. When the Spanish began fighting over the gold, a son of the cacique "volunteered a gem of geographical information worth more than all the gold of the Indies: I will shewe you a region flowing with golde, where you may satisfie your ravening appetites… . When you are passing over these mountains (pointing with his finger towarde the south mountains)…you shall see another sea…" (recorded by Peter Martyr and quoted from Boorstin, 1983, p. 257). In crossing the Cordillera Central, "The dark recesses of the tropical rain forest were like nothing they had known before. Later explorers found that Balboa's route still taxed them to the limits of courage and endurance. In the mid-nineteenth century a French explorer reported that he could not see the sky for eleven days, while

a German botanical expedition, trying to struggle through, lost every man… . After twenty-five days of 'many adventures and great privation' the cordillera was finally crossed. On September 25, 1513, their Quarequa guide pointed them toward a nearby peak. Vasco [Núñez de Balboa] commanded his men to halt while he ascended, and from the top he glimpsed an ocean in the distance. Another four day's trek took them to the shore of this newly discovered ocean" (Boorstin, 1983, p. 257–258). Balboa later planned an expedition into the southern sea, and had actually finished transporting ship-building material across the isthmus, when he was falsely accused of planning to desert the Spanish monarchy and make himself emperor of Peru. A contingent from Spain arrived, including Francisco Pizarro, and, before a defense could be mounted, Balboa was beheaded and his body thrown to the vultures.

9. In most cases, the names Guiana and Guayana are used synonymously, with the former spelling being used by the British and other northern Europeans and the latter by Spanish speakers. Should there be any confusion, however, perhaps the following will help:

> "*Guayana, Guiana*: a physiographic region of northern South America centered on one of the continent's two Precambrian crystalline shields and including much of southern Venezuela, Guyana, Suriname, French Guiana, and a portion of southeastern Colombia and northern Brazil.
>
> *Guayana Shield* (also Guiana Shield, Guyana Shield, Guayanan Shield): the ancient crystalline shield area of northern South America.
>
> *Venezuelan Guayana*: the Venezuelan part of the Guayana region; politically, the Venezuelan states of Amazonas, Bolívar, and Delta Amacuro.
>
> *Guayana Highland(s)* (also Guiana Highlands): the high-elevation portions of the Guayana Shield, usually above 1500 m (also known as Pantepui), although previously used in a broader sense to include lower mountains and even lowland areas.
>
> *Guianas*: the countries of Guyana and Suriname, and the Department of French Guiana.
>
> *Guyana*: an independent country, formerly the colony of British Guiana.
>
> *Dutch Guiana*: now the independent country of Suriname (alternately spelled Surinam).
>
> *Guyana Française*: French spelling of French Guiana, an overseas Department of France." Steyermark et al. (1995, p. xix).

10. A fascinating account of the intrigue, diplomacy, and international economic consequences of attempts of growing coffee in the marginally suitable region of Paraná is given by Mark Pendergrast, 1999, *Uncommon Grounds*, *The History of Coffee and How It Changed the World*, Basic Books, New York (see also footnote 1, Chapter 2; Gómez and Savage, 1983, p. 2).

REFERENCES

Andreae, M. O. et al. (+ 6 authors). 2004. Smoking rain clouds over the Amazon. Science 303: 1337–1342.

Atlas de Cuba. 1978. Instituto Cubano de Geodésia y Cartografía. La Habana, Cuba. (See also the Instituto's Cuba National Atlas [Nuevo Atlas Nacional de Cuba, 1989].)

Bates, H. W. 1930. The Naturalist on the River Amazons. E. P. Dutton, New York. (See also 1892, John Murray, London.)

Blouet, B. W. and O. M. Blouet (eds.). 1993. Latin America and the Caribbean: A Systematic and Regional Survey. 2nd ed. John Wiley & Sons, New York.

Bolay, E. 1997. The Dominican Republic: A Country between Rain Forest and Desert. Margraf Verlag, Weikersheim, Germany.

Bongaarts, J. and R. A. Bulatao (eds.). 2000. Beyond Six Billion: Forecasting the World's Population. National Academy Press, Washington, D.C.

Boorstin, D. J. 1983. The Discoverers. Random House, New York.

Borhidi, A. 1996. Phytogeography and Vegetation Ecology of Cuba. Akadémiai Kiadó, Budapest.

Bryson, R. A. and F. K. Hare (eds.). 1974. Climates of North America. World Survey of Climatology, Vol. 11. Elsevier Science Publishers, Amsterdam.

Bush, M. B. and M. R. Silman. 2004. Observations on late Pleistocene cooling and precipitation in the lowland neotropics. J. Quatern. Sci. 19: 677–684.

Cabrera, A. 1976. Regiones fitogeográficas Argentinas. Enciclopedia Argentina Agricultura y Jardinería. 2nd ed., Tomo II. Editorial Acme, Buenos Aires.

Calsbeek, R. and T. B. Smith. 2003. Ocean currents mediate evolution in island lizards. Nature 426: 552–555.

Cañadas Cruz, L. 1983. El mapa bioclimático y ecológico del Ecuador. Banco Central del Ecuador, Quito.

Carlson, F. A. 1952. Geography of Latin America. Prentice-Hall, New York.

Chapman, F. M. 1929. My Tropical Air Castle: Nature Studies in Panama. D. Appleton, New York.

Clapperton, C. 1993. Quaternary Geology and Geomorphology of South America. Elsevier Science Publishers, Amsterdam.

Clark, K. L., R. O. Lawton, and P. R. Butler. 2000. The physical environment. *In:* N. M. Nadkarni and N. T. Wheelwright (eds.), Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, Oxford, U.K. pp. 15–38.

Coen, E. 1983. Climate. *In:* D. H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago. pp. 35–46.

Crowley, T. J. and G. R. North. 1996. Paleoclimatology. Oxford Monographs on Geology and Geophysics No. 18. Oxford University Press, Oxford, U.K.

Dallman, P. R. 1998. Plant Life in the World's Mediterranean

Climates. University of California Press, Berkeley.
Dickinson, R. E. (ed.). 1987. The Geophysiology of Amazonia: Vegetation and Climate Interactions. John Wiley & Sons, New York.
Donnelly, T. W. et al. (+ 9 authors). 1990. History and tectonic setting of Caribbean magmatism. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 339–374.
Eidt, R. C. 1968. The climatology of South America. *In:* E. J. Fittkau et al. (eds.), Biogeography and Ecology in South America, Vol. 1. Dr. W. Junk, The Hague, The Netherlands. pp. 54–81.
Europa World Yearbook. 1996. Europa Publications Ltd., London.
Famighetti, R. (ed.). 1997. The World Almanac and Book of Facts. World Almanac Books, Mahwah, NJ.
Feely, R. A. et al. (+ 6 authors). 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305: 362–366.
Fisher, M. J. et al. (+ 6 authors). 1994. Carbon storage by introduced deep-rooted grasses in the South American savannas. Nature 371: 236–238.
Fleming, T. H. 1986. Secular changes in Costa Rican rainfall: Correlation with elevation. J. Trop. Ecol. 2: 87–91.
Frost, S. H. and R. L. Langenheim Jr. 1974. Cenozoic Reef Biofacies. Northern Illinois University Press, De Kalb.
García, E. 1987. Perfil Ambiental de la República de Guatemala. ICATA, Guatemala City.
———. 1990. Climas, Map IV.4.10, scale 1:4,000,000. Atlas Nacional de México, vol. II. Instituto Geografía, Universidad Nacional Autónoma de México, México, D.F.
——— and P. Mosiño A. 1968. Los climas de la Baja California. *In:* Comité Nacional Mexicano para el Decenio Hidrológico Internacional. Memoria 1966–1967. México, D.F. pp. 29–54.
Garreaud, R., M. Vuille, and A. C. Clement. 2003. The climate of the Altiplano: Observed current conditions and mechanisms of past changes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 5–22.
Gaussen, H. 1955. Expression des milieux par des formulas écologiques; leur representation cartographique. Coll. Int. Cent. Nat. Rech. Sci. 59: 257–269.
Gentry, A. H. 1986. Species richness and floristic composition of Chocó region plant communities. Caldasia 15: 71–91.
——— (ed.). 1990. Four Neotropical Rainforests. Yale University Press, New Haven, CT.
Glantz, M. H. 2001. Currents of Change: Impacts of El Niño and La Niña on Climate and Society. 2nd ed. Cambridge University Press, Cambridge, U.K.
Gómez, L. D. and J. M. Savage. 1983. Searchers on that rich coast: Costa Rican field biology, 1400–1980. *In:* D. H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago. pp. 1–11.
González-Morán T., R. Rodríquez, and S. A. Cortes. 1999. The Basin of Mexico and its metropolitan area: Water abstraction and related environmental problems. J. S. Amer. Earth Sci. 12: 607–613.
Gottgens, J. F. et al. (+ 5 authors). 2001. The Paraguay–Paraná Hidrovía: Protecting the Pantanal with lessons from the past. BioScience 51: 301–308.
Grace, J. et al. (+ 11 authors). 1995. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993. Science 270: 778–780.
Graham, A. 1999. Late Cretaceous and Cenozoic History of North American Vegetation (North of Mexico). Oxford University Press, Oxford, U.K.
Grau, H. R. et al. (+ 5 authors). 2003. The ecological consequences of socioeconomic and land-use changes in post-agriculture Puerto Rico. BioScience 53: 1159–1168.
Grayum, M. H., B. E. Hammel, and N. Zamora. 2004. El Ambiente Físico/The Physical Environment. *In:* B. E. Hammel, M. H. Grayum, C. Herrera, y N. Zamora (eds.), Manual de Plantas de Costa Rica, Vol. 1. Monogr. Syst. Bot. Missouri Bot. Gard. 97: 51–90.
Grubb, P. J. 1971. Interpretation of the "Massenerhebung" effect on tropical mountains. Nature 229: 44–45.
Haack, H. 1985. Sudamerika, Klima und Vegetation. Geographisch-Kartographische Anstalt, Gotha, Germany. Scale 1/9,000,000.
Haffer, J. 1970. Geologic–climatic history and zoogeographic significance of the Urabá region in northwestern Colombia. Caldasia 10: 603–636.
Hastings, J. R. and R. M. Turner. 1965. Seasonal precipitation regimes in Baja California, Mexico. Geogr. Ann., A. Phys. Geogr. 47: 204–223.
Heckman, C. W. 1998. The Pantanal of Poconé: Biota and Ecology in the Northern Section of the World's Largest Pristine Wetland. Kluwer Academic Publishers, Boston.
Herrera, W. 1985. Clima de Costa Rica. *In:* L. D. Gómez (ed.), Vegetación y Clima de Costa Rica. Editorial de la Universidad Estatal a Distancia, San José, Costa Rica.
Holmgren, M., M. Scheffer, E. Ezcurra, J. Gutierrez, and G. M. J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends Ecol. Evol. 16: 89–94.
Hunter, B. (ed.). 1997. The Statesman's Year Book for the Year 1997–1998. St. Martin's Press, New York.
Isacks, B. L. 1988. Uplift of the central Andean Plateau and bending of the Bolivian Orocline. J. Geophys. Res. 93: 13,841–13,854.
Islebe, G. A., A. Valázquez, and A. M. Cleef. 1995. High elevation coniferous vegetation of Guatemala. Vegetatio 116: 7–23.
Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Amer. Nat. 101: 233–249.
Junk, W. J. and C. Nunes de Cunha. 2005. Pantanal: A large South American wetland at a crossroads. Ecol. Engin. 24: 391–401.
Kleidon, A. and M. Heimann. 1999. Deep-rooted vegetation, Amazon deforestation, and climate: Results from a mod-

eling study. Global Ecol. Biogeogr. 8: 397–405.
Koren, I., Y. J. Kaufman, L. A. Remer, and J. V. Martins. 2004. Measurement of the effect of Amazon smoke on inhibition of cloud formation. Science 303: 1342–1345.
Kuhry, P. 1988. Palaeobotanical-palaeoecological studies of the tropical high Andean peat bog sections (Cordillera Oriental, Colombia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 55: 19–72.
Ladd, J. W., T. L. Holcombe, G. K. Westbrook, and N. T. Edgar. 1990. Caribbean marine geology: Active margins of the plate boundary. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 261–290.
Lamb, S. 2004. Devil in the Mountain: A Search for the Origin of the Andes. Princeton University Press, Princeton, NJ.
Lauer, W. 1973. The altitudinal belts of the vegetation in the central Mexican highlands and their climatic conditions. Arctic Alpine Res. 5: 99–113.
Lawton, R. O., U. S. Nair, R. A. Pielke Sr., and R. M. Welch. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. Science 294: 584–587.
Lewis, W. M., Jr., S. K. Hamilton, M. A. Lasi, M. A. Rodríguez, and J. F. Saunders III. 2000. Ecological determinism on the Orinoco floodplain. BioScience 50: 681–692.
Marengo, J. A. and J. C. Rogers. 2001. Polar air outbreaks in the Americas: Assessments and impacts during modern and past climates. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 31–51.
Martínez, I., D. Rincon, Y. Yokoyama, and T. Barrows. 2006. Foraminifera and coccolithophorid assemblage changes in the Panama Basin during the last deglaciation: Response to sea-surface productivity induced by a transient climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 234: 114–126.
Martyn, D. 1992. Climates of the World. Developments in Atmospheric Science 18. Elsevier Science Publishers, Amsterdam.
McCullough, D. 1977. The Path between the Seas: The Creation of the Panama Canal, 1870–1914. Simon & Schuster, New York.
McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.). 1994. La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago.
Meir, P., R. Cox, and J. Grace. 2006. The influence of terrestrial ecosystems on climate. Trends Ecol. Evol. 21: 254–260.
Minter, J. E. 1948. The Chagres: River of Western Passage. Rinehart, New York.
Moorehead, A. 1969. Darwin and the Beagle. Harper & Row, New York.
Müllerried, F. K. G. 1957. Geología de Chiapas. Gobierno Constitucional del Estado de Chiapas, Tuxtla Gutiérrez, México.
Myers, C. W. 1969. The ecological geography of cloud forest in Panama. Amer. Mus. Novit. 2396: 1–52.
Myers, N. 2001. Playing the numbers game. Nature 410: 631–632.
Naranjo, P. 1981. El Clima del Ecuador. Casa de la Ecuadoriana, Quito.
Nature. 2004. Fishermen call an end to siege. Nature 428 (March 2004): 8–94.
Navarro-González, R. et al. (+ 11 authors). 2003. Mars-like soils in the Atacama Desert, Chile, and the dry limit of microbial life. Science 302: 1018–1021. [See Letters and response, Science 306: 1289, 19 Nov. 2004.]
O'Neill, B. C., F. L. MacKellar, and W. Lutz. 2001. Population and Climatic Change. Cambridge University Press, Cambridge, U.K.
Orvis, K. H. 2003. The highest mountain in the Caribbean: Controversy and resolution via GPS. Caribbean J. Sci. 39: 378–380.
Osborne, P. L. 2000. Tropical Ecosystems and Ecological Concepts. Cambridge University Press, Cambridge, U.K.
Pagani, M., J. C. Zachos, K. H. Freeman, B. Tipple, and S. Bohaty. 2005. Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. Science 309: 600–603. [Atmospheric CO_2 levels fell from 1500 parts per million to modern levels of 300 parts per million from 35 to 25 million years ago, coincident with the buildup of ice in Antarctica.]
Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimatic envelope models useful? Global Ecol. Biogeogr. 12: 361–371.
Perry, E., L. Marin, J. McClain, and G. Velázquez. 1995. Ring of cenotes (sinkholes), northwest Yucatán, México: Its hydrologic characteristics and possible association with the Chixulub impact crater. Geology 23: 17–20.
Peterson, L. C. and G. H. Haug. 2006. Variability in the mean latitude of the Atlantic Intertropical Convergence Zone as recorded by riverine input of sediments to the Cariaco Basin (Venezuela). Palaeogeogr. Palaeoclimatol. Palaeoecol. 234: 97–113.
Por, F. D. 1995. The Pantanal of Mato Grosso (Brazil): World's Largest Wetlands. Kluwer Academic Publishers, Boston.
Porrut, P. 1983. Los climas del Ecuador—fundamentos explicativos. CEDIG Documentos de Investigación, Quito 4: 7–41.
Porter, D. M. 1973. The vegetation of Panama: A review. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 167–201.
Pott, A. and V. J. Pott. 1997. Plants of Pantanal. Embrapa, Corumbá, Brazil.
Poveda, G., P. R. Waylen, and R. S. Pulwarty. 2006. Annual and inter-annual variability of the present climate in northern South America and southern Mesoamericana. Palaeogeogr. Palaeoclimatol. Palaeoecol. 234: 3–27.
Richards, P. W. 1996. The Tropical Rain Forest. 2nd ed. Cam-

bridge University Press, Cambridge, U.K.
Rymer, R. 2004. Saving the music tree. Smithsonian 35: 52–58, 61–63.
Sabine, C. L. et al. (+ 14 authors). 2004. The ocean sink for anthropogenic CO_2. Science 305: 367–371.
Saleska, S. R. et al. (+ 17 authors). 2003. Carbon in Amazon forests: Unexpected seasonal fluxes and disturbance-induced losses. Science 302: 1554–1557.
Sánchez, O. S. and G. A. Islebe. 1999. Hurricane Gilbert and structural changes in a tropical forest in south-eastern Mexico. Global Ecol. Biogeogr. 8: 29–38.
Sanford, R. L., Jr., P. Paaby, J. C. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. *In:* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago. pp. 19–33.
Schiermeier, Q. 2005. That sinking feeling. Nature 435: 732–733.
Schubert, C. 1972. Geomorphology and glacier retreat in the Pico Bolívar area, Sierra Nevada de Mérida, Venezuela. Z. Gletscherkunde Glazialgeologie 8: 189–202.
Schwerdtfeger, W. 1976. Climates of Central and South America. World Survey of Climatology Vol. 12. Elsevier Science Publishers, Amsterdam.
Sioli, H. 1984. 1. Introduction: History of the discovery of the Amazon and of research of Amazonian waters and landscapes. *In:* H. Sioli (ed.), The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 1–13.
Smith, L. C. et al. (+ 7 authors). 2004. Siberian peatlands a net carbon sink and global methane source since the early Holocene. Science 303: 353–356.
Steinhauser, F. 1979. Climate Atlas of North and Central America. WMO, UNESCO, Cartographia. Geneva, Switzerland.
Steyermark, J. A., P. E. Berry, and B. K. Holst (eds.). 1995. Flora of the Venezuelan Guayana, Vol. 1. Introduction. Missouri Botanical Garden, St. Louis/Timber Press, Portland, OR.
Swarts, F. A. (ed.). 2000. The Pantanal: Understanding and Preserving the World's Largest Wetland. Paragon House, St. Paul, MN.
The Oxford Atlas of the World. 1997. Oxford University Press, Oxford, U.K.
The Times Atlas of the World. 1995. Times Books, London.
Trewartha, G. T. and L. H. Horn. 1980. An Introduction to Climate. 5th ed. McGraw-Hill Book Company, New York.
Tuomisto, H. et al. (+ 5 authors). 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.
U.S. Board on Geographic Names. 1956 (et seq.). Office of Geography, Department of the Interior, Washington, D.C.
U.S. Department of Commerce/NOAA/National Climatic Data Center. 1991. World Weather Records 1971–1980, Vol. 3. West Indies, South and Central America. U.S. Department of Commerce, Washington, D.C.
Walsh, R. P. D. 1996. Climate. *In:* P. W. Richards, The Tropical Rain Forest, an Ecological Study. 2nd ed. Cambridge University Press, Cambridge, U.K. pp. 159–205.
Walter, H. and H. Lieth. 1960–1967. Klimadiagramm-Weltatlas. G. Fischer Verlag, Jena, Germany.
Weidmann, K. (with text by Manuel Pérez Vila and Otto Huber). 1986. La "Gran Sabana." Oscar Todtmann Editores, Caracas, Venezuela.
Wiggins, I. L. 1980. Flora of Baja California. Stanford University Press, Stanford, CA.
Wilke, J. W. (ed.; C. Komisaruk and J. Guadalupe Ortega, co-eds.). 1996. Statistical Abstract of Latin America, Vol. 32. Latin American Center Publications, UCLA/University of California Press, Los Angeles.
Wikelski, M., L. M. Romero, and H. L. Snell. 2001. Marine iguanas oiled in the Galápagos. Science 292: 437–438.
Zebrowski, E., Jr. 2002. The Last Days of St. Pierre: The Volcanic Disaster that Claimed Thirty Thousand Lives. Rutgers University Press, New Brunswick, NJ.
Zuloaga, F. O. and O. Morrone (eds.). 1999. Catálogo de las Plantas Vasculares de la República Argentina. Part II, Fabaceae-Zygophyllaceae (Dicotyledoneae). Monogr. Syst. Bot. Missouri Bot. Gard. 74.

ADDITIONAL REFERENCES/GENERAL READINGS/ ELECTRONIC ADDRESSES

Alley, R. B., P. U. Clark, P. Huybrechts, and I. Joughin. 2005. Ice-sheet and sea-level changes. Science 310: 456–460.
Allsopp, R. 1996. Dictionary of Caribbean English Usage. Oxford University Press, Oxford, U.K.
Alverson, K. et al. (+ 8 authors). 2001. A global paleoclimate observing system. Science 293: 47–48.
American Institute of Physics, Center for History of Physics. The Discovery of Global Warming. http://www.aip.org/history/climate. [Hyperlinked essays, references, publications, and links to pertinent sites.]
Archer, D. 2003. Who threw that snowball? Science 302: 791–792. [Discusses the role of ocean $CaCO_3$ precipitation in regulating global climate.]
AVHRR Image Gallery. The Johns Hopkins University Applied Physics Laboratory, Ocean Remote Sensing Group. http://fermi.jhuapl.edu/avhrr/gallery. [Satellite passes, surface temperature, coastal views, landforms, ice and snow, clouds and storms, interesting observations, observations of forest fires.]
Bassett, S. E., G. A. Milne, J. X. Mitrovica, and P. U. Clark. 2005. Ice sheet and solid Earth influences on far-field sea-level histories. Science 309: 925–928. [A model with a stiff mantle and rapid melting of Antarctic ice sheets matches well the rise in sea level after the Last Glacial Maximum observed at tropical Pacific sites.]
BBC-TV. 1997. Spirits of the Jaguar—Hunters of the Ca-

ribbean Sea. Nature Video Library. BBC-TV, London/WNET, Boston.

Berner, R. A. 2003. The long-term carbon cycle, fossil fuels and atmospheric composition. Nature 426: 323–326.

Bradshaw, W. E. and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. Science 312: 1477–1478. [Recent, rapid climate change is driving evolution, as organisms adapt to altered seasonal events rather than to the direct effects of increasing temperatures.]

Brook, E. J. 2005. Tiny bubbles tell all. Science 310: 1285–1287.

Brown, K. 2002. Water scarcity: Forecasting the future with spotty data. Science 297: 926–927. [See also Finnegan, 2002.]

Browne, J. 2003. Charles Darwin: The Power of Place. Princeton University Press, Princeton, NJ.

Burroughs, W. J. 2005. Climate Change in Prehistory: The End of the Reign of Chaos. Cambridge University Press, Cambridge, U.K.

Cazenave, A. 2006. How fast are the ice sheets melting? Science 314: 1250–1252.

Changnon, S. A. 2000. El Niño 1997–1998: The Climate Event of the Century. Oxford University Press, Oxford, U.K.

Chelton, D. B., M. G. Schlax, M. H. Freilich, and R. F. Milliff. 2004. Satellite measurements reveal persistent small-scale features in ocean winds. Science 303: 978–983.

Chen, J L., C. R. Wilson, and B. D. Tapley. 2006. Satellite gravity measurements confirm accelerated melting of Greenland ice sheet. Science 313: 1958–1960.

Cle, D. 2006. Climate change demands action, says U.K. report. Science 311: 592.

Colinvaux, P. 2005. Coping with interesting times. Nature 437: 479. (Review of T. E. Lovejoy and L. Hanna [eds.]. 2005. Climate Change and Biodiversity. Yale University Press, New Haven, CT.) [Unless we take action urgently, climate change could spell disaster for a wide range of living species.]

Cook, A. J., A. J. Fox, D. G. Vaughan, and J. G. Ferrigno. 2005. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. Science 308: 541–544. [Trends in 244 marine glacier fronts for the past 61 years show that 87% have retreated.]

Cox, J. D. 2005. Climate Crash: Abrupt Climate Change and What It Means for Our Future. Joseph Henry Press, Washington, D.C.

Craw, R. C., J. R. Grehan, and M. J. Heads. 1999. Panbiogeography: Tracking the History of Life. Oxford University Press, Oxford, U.K.

Crowley, T. J. 2004. Review: S. R. Weart, 2003, The Discovery of Global Warming. Harvard University Press, Cambridge, MA. Science 304: 685–686.

Cruz-Reyna, S. and C. Siebe. 1997. The giant Popocatépetl stirs. Nature 388: 227.

Davis, C. H., Y. Li, J. R. McConnell, M. K. Frey, and E. Hanna. 2005. Snowfall-driven growth in East Antarctic ice sheet mitigates recent sea-level rise. Science 308: 1898–1901.

Dittert, N., M. Diepenbroek, and H. Grobe. 2001. Scientific data must be made available to all. Nature 414: 393. [Regarding data for global climate change models.]

Dorf, E. 1945. Observations on the preservation of plants in the Parícutin area. Trans. Amer. Geophys. Union 26: 257–260.

———. 1951. Lithologic and floral facies in the Parícutin ash deposits, Mexico. Trans. New York Acad. Sci. 13: 317–320.

Dowdeswell, J. 2006. The Greenland ice sheet and global sea-level rise. Science 311: 963–964. [Accelerating flow suggests current estimates of sea-level rise may be too low.]

Dusheck, J. 2002. It's the ecology, stupid. Nature 418: 578–579.

Ebach, M. C. and R. S. Tangney. 2007. Biogeography in a Changing World. CRC Press, Taylor & Francis Group, Boca Raton, FL.

Environmental History of Latin America. http://www.stanford.edu/group/LAEH/. [Bibliography, environmental history of Latin America; conservation, politics, policies.]

Fagen, B. 2000. The Little Ice Age. Basic Books (Perseus Books Group), New York.

Falkowski, P. G. et al. (+ 8 authors). 2005. The rise of oxygen over the past 205 million years and the evolution of large placental mammals. Science 309: 2202–2204. [The atmosphere concentration of O_2 has risen irregularly from ~10% in the Early Jurassic, 23% in the Tertiary, to the present 21%.]

Feddema, J. J. et al. (+ 6 authors). 2005. The importance of land-cover change in simulating future climates. Science 310: 1674–1678.

Finnegan, W. 2002. Letter from Bolivia, Leasing the rain—the world is running out of fresh water, and the fight to control it has begun. The New Yorker, 8 April 2002. [The Cochabamba, Bolivia, water war; see also Brown, 2002.]

Flannery, T. 2005. The Weather Makers: How Man Is Changing the Climate and What It Means for Life on Earth. Allen Lane, London.

Foukal, P., G. North, and T. Wigley. 2004. A stellar view on solar variations and climate. Science 306: 68–69.

García, E. 1970. Los climas del estado de Veracruz. Anales Inst. Biol. Univ. Nac. Autón. México, Bot. 41: 3–42.

Gilbert, S. 2001. Ecological developmental biology: Developmental biology meets the real world. Dev. Biol. 233: 1–12.

Giles, J. 2002. When doubt is a sure thing. Nature 418: 476–478. [Communication of uncertainty in climatology.]

———. 2006. How much will it cost to save the world? Nature 442: 6–7.

Glantz, M. H. 2001. Currents of Change: Impacts of El Niño and La Niña on Climate and Society. Cambridge University Press, Cambridge, U.K.

Greenland, D., D. G. Gooden, and R. C. Smith (eds.). 2003. Climate Variability and Ecosystem Response at Long-

term Ecological Research Sites. Oxford University Press, Oxford, U.K.

Hansen, B., S. Østerhus, D. Quadfasel, and W. Turrell. 2004. Already the day after tomorrow? Science 305: 953–954. [Effect of global warming on thermohaline circulation and world climates.]

Hansen, J. et al. (+ 14 authors). 2005. Earth's energy imbalance: Confirmation and implication. Science 308: 1431–1435. [Earth is now absorbing nearly 1 W/m^2 more energy from the sun than it is emitting to space, portending further warming even if greenhouse gas levels were to immediately stabilize.]

Harvey, L. D. D. 2000. Global Warming—The Hard Science. Prentice Hall, New York.

Hay, W. W. 1996. Tectonics and climate. Geol. Rundschau. 85: 409–437.

———, R. M. DeConto, and Ch. N. Wold. 1997. Climate: Is the past the key to the future? Geol. Rundschau. 86: 471–491.

Holbourn, A., W. Kuhnt, M. Schulz, and H. Erlenkeuser. 2005. Impacts of orbital forcing and atmospheric carbon dioxide on Miocene ice-sheet expansion. Nature 438: 483–487.

Hulshof, O. K. and A. A. Manten. 1971. Bibliography of actuopalynology, 1671–1996. Rev. Palaeobot. Palynol. 12: 1–243.

International Paleontological Association Electronic Database. http://ipa.geo.ku.edu.

Islebe, G. A. 1996. Vegetation, phytogeography and paleo-ecology of the last 20,000 years of montane Central America. Hugo de Vries Laboratory, University of Amsterdam, Amsterdam. [Papers from Islebe's doctoral dissertation on the modern and late Quaternary montane vegetation of Guatemala and Costa Rica.]

Jansson, R. and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Ann. Rev. Ecol. Syst. 33: 741–777.

Jauregui, E. 1997. Climate changes in Mexico during the historical and instrumented periods. Quatern. Int. 43/44: 7–17.

Kanipe, J. 2006. A cosmic connection. Nature 443: 141–143. [Physicists and climate scientists have long argued over whether changes to the sun affect the Earth's climate. A cloud chamber could help clear up the dispute.]

Kelley, K. A. 2004. Wind data: A promise in peril. Science 303: 962–963.

Kemp, M. 2005. Inventing an icon, Hans Joachim Schellnhuber's map of global 'tipping points' in climate change. Nature 437: 1238.

Kennedy, D. 2003. The policy drought on climatic change. Science 299: 309.

———. 2006. New year, new look, old problem. Science 311: 15.

———. Acts of God? Science 311: 303.

Kerr, R. A. 1997. Climate-evolution link weakens. Science 276: 1968.

———. 2004a. Three degrees of consensus. Science 305: 932–934. [Climate researchers are finally homing in on just how bad greenhouse warming could get—and it seems increasingly unlikely that we will escape with a mild warming.]

———. 2004b. A bit of icy Antarctica is sliding toward the sea. Science 305: 1897.

———. 2005a. Millennium's hottest decade retains its title, for now. Science 307: 828–829.

———. 2005b. Confronting the bogeyman of the climate system. Science 310: 432–433.

———. 2005c. The Atlantic conveyor may have slowed, but don't panic yet. Science 310: 1403–1405.

———. 2006a. No doubt about it, the world is warming. Science 312: 825.

———. 2006b. Latest forecast: Stand by for a warmer, but not scorching, world. Science 312: 351.

———. 2006c. Opening the door to a chilly climate regime. Science 312: 350.

King, D. A. 2004. Climate change science: Adapt, mitigate, or ignore? Science 303: 176–177.

Kintische, E. 2005. Global warming skeptic argues U.S. position in suit. Science 308: 482. ["Impacts…will include sea level rise,…disturbances of ecosystems…[and] an accelerated reduction of water storage in winter snowpack," Michael MacCracken, in brief for plaintiffs; "Significant questions still remain as to [whether] this…rise in air temperature can be attributed to anthropogenic increases in greenhouse gas concentrations," David Legates, in brief for government.]

Kolbert, E. 2006. Butterfly lessons. The New Yorker, 9 January 2006: 32–39.

Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304: 1623–1627. [Part of special section, Soils—The Final Frontier.]

Lawler, A. 2004. Stormy forecast for climate science. Science 305: 1094–1097.

Lincoln, T. 2004. Glacial pace picks up. Nature 431: 519.

Linden, E. 2006. The Winds of Change: Climate, Weather, and the Destruction of Civilizations. Simon & Schuster, New York.

Lovejoy, T. E. and L. Hanna (eds.). 2005. Climate Change and Biodiversity. Yale University Press, New Haven, CT.

Lutz, W., W. Sanderson, and S. Scherbov. 1997. Doubling of world population unlikely. Nature 387: 803–805.

———, ———, ———. 2001. The end of world population growth. Nature 412: 543–545.

Mason, B. 2004. The hot hand of history. Nature 427: 582–583.

Mayorga, E. et al. (+ 7 authors). 2005. Young organic matter as a source of carbon dioxide outgassing from Amazonian rivers. Nature 436: 538–541.

McPhaden, M. J., S. E. Zebiak, and M. H. Glantz. 2006. ENSO as an integrating concept in earth science. Science 314: 1740–1745.

Meehl, G. A. and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305: 994–997. ["A global coupled model shows that there is a distinct geographic pattern to future changes in heat waves. Model results for areas of Europe and North America…show that future heat waves will become more intense, more frequent, and longer-lasting in the second half of the 21st century."]

——— et al. (+ 7 authors). 2005. How much more global warming and sea level rise? Science 307: 1769–1772.

Miller, K. G. et al. (+ 9 authors). 2005. The Phanerozoic record of global sea-level change. Science 310: 1293–1298.

NASA Earth Observations. http://earthobservatory.nasa.gov. [e.g., growth of the southern ozone hole, paleoclimatology, sea temperatures, clouds, fire, vegetation, CO_2 sinks, polar ice, articles, news.]

NOAA Paleoclimatology, NOAA Satellite and Information Service. www.ngdc.noaa.gov/paleo/ctl/index.html. [Global warming, climatic variation and human history/evolution, ice cores, tree rings, Anasazi civilization and drought.]

National Geospatial-Intelligence Agency GEOnet Names Server. http://earth-info.nga.mil/gns/html/index.html. [U.S. Board Geographic Names locations, coordinates.]

Nature. 2006. Reaching a tipping point. Nature 441: 785. [A popular new paradigm for the nature of [climate] change pertains more to the social and political worlds than it does to the physical one.]

Normile, D. 2005. Japan's new ship sets standard as modern, floating laboratory. Science 307: 1552–1553. [*Chikyu* is the latest in ocean research vessels following the *Challenger* (1872–1876), *Glomar Challenger*, *JOIDES Resolution*, and *Atlantis*, which carries the submersible Alvin and a digital camera mounted on the remotely operated vehicle Argoll.]

Oreskes, N. 2004. The scientific consensus on climate change. Science 306: 1686. [Without substantial disagreement, scientists find human activities are heating the Earth's surface.]

Osborn, T. J. and K. R. Briffa. 2004. The real color of climate change? Science 306: 621–622.

Patel, S. S. 2006. A sinking feeling. Nature 440: 734–736. [Floods and rising seas.]

Patz, J. A., D. Campbell-Lendrum, T. Holloway, and J. A. Foley. 2005. Impact of regional climate change on human health. Nature 438: 310–317.

PBS Home Video/South Carolina Educational Television. 2005. Global Warming, the Signs and the Science.

Peeters, F. J. C. et al. (+ 7 authors). 2004. Vigorous exchange between the Indian and Atlantic oceans at the end of the past five glacial periods. Nature 430: 661–665.

Philander, S. G. 2004. Our Affair with El Niño: How We Transformed an Enchanting Peruvian Current into a Global Climate Hazard. Princeton University Press, Princeton, NJ. [See review in Nature 429, 10 June 2004: 605–606.]

Pielke, R. A., Sr. 2005. Land use and climate change. Science 310: 1625–1626.

Pinholster, G. 2004. Facing the impact of global warming. Science 304: 1921–1922.

Planiglobe Beta. http://www.planiglobe.com. [Create maps, e.g., distribution maps, by typing in latitude and longitude.]

Poinar, G. O., Jr. 1992. Life in Amber. Stanford University Press, Stanford, CA.

Pugh, J. C. 2003. New climate-change data place policymakers in the hot seat. BioScience 53: 542–543.

Raymond, P. A. 2005. The age of the Amazon's breath. Nature 436: 469–470.

Rosenzweig, C. and D. Hillel. 1998. Climate Change and the Global Harvest: Potential Impacts of the Greenhouse Effect on Agriculture. Oxford University Press, Oxford, U.K.

Ruddiman, W. F. 2001. Earth's Climate: Past and Future. W. H. Freeman & Sons, New York.

———. 2005. Plows, Plagues and Petroleum: How Humans Took Control of Climate. Princeton University Press, Princeton, NJ.

———. 2006. Nicholas J. Shackleton (1937–1906). Science 312: 711.

Schiermeler, Q. 2004. A rising tide. Nature 428: 114–115. [The ice covering Greenland holds enough water to raise the oceans seven meters—and it's starting to melt. How far will it go?]

———. 2006. Putting back the carbon (the hundred billion tonne challenge). Nature 442: 620–623.

———. 2007. The new face of the Arctic. Nature 446: 133–135.

———. 2007. No solar hiding places for greenhouse skeptics. Nature 448: 8.

Schneider, S. H. 2001. What is "dangerous" climate change? Nature 411: 17–19.

Scopus. http://www.scopus.com. [Scopus, a comprehensive science-specific search engine.]

Siegert, F., G. Ruecker, A. Hinrichs, and A. A. Hoffmann. 2001. Increased damage from fires in logged forests during droughts caused by El Niño. Nature 414: 437–440.

Sioli, H. 1966. General features of the delta of the Amazon. *In:* Proceedings of the Dacca Symposium, Humid Tropics Research—Scientific Problems of the Humid Tropical Zone Deltas and Their Implications. UNESCO, Paris. pp. 381–390.

Smith, H. J. 2005. Climate Science: Rete Mirabile. Science 307: 1015. [CO_2 and vegetation on geologic time scales; article: Proc. Natl. Acad. Sci. U.S.A. 102.]

Smith, L. C., Y. Sheng, G. M. MacDonald, and L. D. Hinzman. 2005. Disappearing Arctic lakes. Science 308: 1429. [Satellite observations show that more than 1000 of the 10,000 lakes in Siberia have drained over the past 30 years as permafrost beneath them thawed.]

Smith, N. J. H. 1999. The Amazon River Forest: A Natural History of Plants, Animals, and People. Oxford Univer-

sity Press, Oxford, U.K.
Spahni, R. et al. (+ 10 authors). 2005. Atmospheric methane and nitrous oxide of the late Pleistocene from Antarctica ice cores. Science 310: 1317–1321.
Stone, R. and J. Bohannon. 2006. Global warming: U.N. conference puts spotlight on reducing impact of climate change. Science 314: 1224–1225.
Thomas, C. D. et al. (+ 18 authors). 2004. Extinction risk for climate change. Nature 427: 145–148.
Thomas, R. et al. (+ 17 authors). 2004. Accelerated sea-level rise from West Antarctica. Science 306: 255–258.
Time Magazine. 2006. Special Report: Global Warming. 3 April 2006.
Turner, J., T. A. Lachlan-Cope, S. Colwell, G. J. Marshall, and W. M. Connolley. 2006. Significant warming of the Antarctic winter troposphere. Science 311: 1914–1917. [The wintertime temperature of the Antarctic troposphere has risen by more than 0.5° C per year over the past 30 years, a rate higher than that for any other region.]
United Nations. 1999. Long-range World Population Projections: Based on the 1998 Revisions. United Nations, New York (ESA/p/wp.153).
Vaughan, D. G. 2005. How does the Antarctic ice sheet affect sea level rise? Science 308: 1877–1878. [See article, Davis et al., 2005.]
TravelJournals.net. http://www.traveljournals.net/explore. [Country-by-country alphabetical listings of coordinates.]
Vecchi, G. A. et al. (+ 5 authors). 2006. Weakening of tropical Pacific atmospheric circulation due to anthropogenic forcing. Nature 441: 73–76.
Walker, G. 2006. The tipping point of the iceberg. Nature 441: 802–805.
Walther, G.-R., C. A. Burga, and P. J. Edwards (eds.). 2001. "Fingerprints" of Climate Change: Adapted Behavior and Shifting Species Ranges. Kluwer Academic Publishers, Dordrecht, The Netherlands.
——— et al. (+ 8 authors). 2002. Ecological responses to recent climate change. Nature 416: 389–395.
Wara, M. W., A. C. Ravelo, and M. L. Delaney. 2005. Permanent El Niño-like conditions during the Pliocene warm period. Science 309: 758–761.
Weart, S. P. 2003. The Discovery of Global Warming. Harvard University Press, Cambridge, MA.
Weil, T. E., J. K. Black, H. I. Blutstein, K. T. Johnson, D. S. McMorris, and F. P. Munson. 1985. Haiti: A Country Study. Area Handbook Series. Secretary of the Army, Washington, D.C.
Weltzin, J. F. et al. (+ 6 authors). 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. BioScience 53: 941–952.
Whitney R. Harris World Ecology Center at the University of Missouri–St. Louis. http://www.umsl.edu/~biology/hwec/.
Wigley, T. M. L. 2005. The climate change commitment. Science 307: 1766–1769.
Witze, A. 2006. Bad weather ahead. Nature 441: 564–566. [Scientists and policymakers are battling over whether global warming is making hurricanes more destructive; see also, The gathering storm, p. 549.]
Zimov, S. A., E. A. G. Schuur, and F. S. Chapin III. 2006. Permafrost and the global carbon budget. Science 312: 1612–1613. [Climate warming will thaw permafrost, releasing trapped carbon from this high-latitude reservoir and further exacerbating global warming.]

Chapter 2

CONSTRUCTING THE LANDSCAPE

Late Cretaceous and Cenozoic Geology of Latin America

Geologic events, geomorphic structures, and sediment types offer clues to vegetation history and to the environment prevailing at the depositional sites of fossil floras. There is geophysical-tectonic evidence for landscape evolution through mountain building, emergence and foundering of land bridges, and the collision and separation of continents and land fragments; geomorphic evidence for volcanism, glaciation, rates of stream flow, valley incisions on land and on the continental slope, changes in lake levels, marine inundations and regressions, and bollide impacts; and sedimentological and geochemical evidence for the prevailing climates from evaporites, charcoal, bauxite, dust, amounts of terrestrial minerals washed into marine basins, and minerals of extraterrestrial origin in Earth sediments. Each reveals the dynamicism of the landscape and the changing habitats within which the organisms evolve, migrate, and recombine into assemblages of ever-changing distribution and composition. The evidence is preserved in the same rocks that yield the plant fossils, and it is a valuable context for reconstructing vegetation history.

The sequence of regional coverages follows that used for the geography of Latin America—Mexico, the Antilles, Central America, and South America. Additional details on local depositional environments and stratigraphy are provided in the discussion of the individual floras (Chapters 4–7).

A note on the Quaternary:

"Some simply describe the past 23 million years as the Neogene Period. But others invoke an extra period—the Quaternary—which follows the Neogene and began around 2 million years ago" (Giles, 2005). A seven-year international project was set up to develop a definitive geological timescale (Whitfield, 2004). "But as the scale was being developed, Quaternary researchers learnt that their period had disappeared—absorbed by the Neogene. The result was a lot of angry geologists. An eight-member task force, set up last August by the International Commission on Stratigraphy (ICS), the organization that coordinated the timescale, and the International Union for Quaternary Research, voted last week to retain the name Quaternary in some form, and to define its onset as 2.6 million years ago." (Giles, 2005)

MEXICO

The geology of Mexico has been outlined by de Cserna (1989), Ferrusquía-Villafranca (1993), and Ferrusquía-Villafranca et al. (2005); the present review is based primarily on these summaries. Kellum (1944) earlier studied the geology of northern Mexico, and Ortega-Gutiérrez et al. (1992) have published the latest revised geologic map of the country. In addition, de Cserna (1990) has compiled a history of geological studies that includes a reproduction of the first geologic map of Mexico published in 1889. As he notes, most investigations, including modern ones, are reconnaissance in nature, or focus on sites with economically important deposits, and there is no modern synthesis of the geology of the country.

Baja California and Northwestern Mainland Mexico—In the Middle and Late Cretaceous, land that would eventually form present-day Baja California was part of a volcanic island arc located along the eastern edge of the old Farallon Plate, precursor of the Pacific Plate, and now mostly subducted beneath North America (Fig. 2.1). The current geology of the peninsula reflects its Late Cretaceous volcanic origin. The central core of northern Baja California (Peninsular Ranges) is composed of crystalline plutonic (= formed at great depth) and metamorphic rocks, and in the south there are extensive volcanics. The most striking of the lava flows are around Volcán Las Tres Virgenes in east-central Baja California. As a result of subduction and the movement of North America westward from the Mid-Atlantic Ridge, the arc became accreted onto the North American Plate in the Oligocene (35.4–23.3 Ma), initially in the vicinity of Sinaloa-Nayarit. After the collision, subduction ceased, a spreading center developed in the present-day Gulf of California at ~29 Ma, and the Gulf continued to open and was further inundated during the Miocene (23.3–6.7 Ma). The transfer of Baja California to the Pacific Plate by northward extension of the spreading center was completed by ~5 Ma. The Pacific Plate, with Baja California, is currently

moving northward relative to the North American Plate at ~5 cm/yr along the San Andreas Fault. Baja California is being elevated at a rate of ~100 mm/Kyr, it has moved northward ~280 km since the Miocene, and in 50 Ma it will be located off the coast of Alaska.

Plate movement continued throughout the Tertiary, and during the process several land fragments were carried with the Pacific Plate from the south and accreted onto the coast of the western United States. Some of these contain fossil floras such as the Miocene Mint Canyon flora of southern California. This flora originally was part of the coastal community of northwestern Mexico. Thus, species lists for the Mint Canyon flora of present-day southern California actually record the Miocene vegetation of northwestern Mexico.

The adjacent mainland in northwestern Sonora includes the oldest known outcrop rocks in Mexico (Precambrian, 1750 Ma). The region was uplifted near the end of the Middle Cretaceous and emerged by the Early Tertiary. It has a basin and range structure of horsts (tilted or uplifted crustal blocks) and grabens (downfaulted basins) like that of the Basin and Range Province of the western United States, and the similarity reflects a related and contemporary history. The low local sierras of northwestern mainland Mexico are between 200 and 1000 m in average elevation and reach a maximum of ~2200 m. They are a product of subduction and compression forces generated by sea-floor spreading in the Gulf of California. The region also includes several island arcs that have accreted onto the mainland further complicating its geologic history (Pérez-Segura & Jacques-Ayala, 1991).

Altiplanicie—Sea level in the Cenomanian (early Late Cretaceous, ~99 Ma) was up to ~300 m higher than at present, due primarily to lower landscapes, increased production of ocean crust (e.g., the Aptian Ontong–Java Plateau), the absence of glaciers, and thermal expansion of the warmer ocean. During that time much of the Altiplanicie was covered by marine waters. Carbonate platforms reached their maximum expanse in the Gulf of Mexico during the Barremian to Albian (~125–95 Ma; Lehmann et al., 1999). In some parts the waters were deep as, for example, along the Chihuahuan Trough. There were also emergent lands, such as the Tamaulipas Peninsula extending southeast from the Big Bend region of the Río Grande del Norte. Reef-forming corals lived in shallow waters of present-day Coahuila along the margin of the epicontinental sea that covered much of northern interior of Mexico, the Yucatán Peninsula, and the Isthmus of Tehuantepec. This sea extended through mid-continent United States, and in the Cenomanian it connected the Gulf of Mexico with the Arctic Ocean. The mostly low relief and extensive inundation, together with high residual atmospheric CO_2 from previous active plate movement, contributed to low thermal gradients and equable climates that extended across much of Mexico and northern North America.

Figure 2.2. Northeastern Mesa Central looking east toward the edge of the plateau escarpment. Tributaries of the Río Meztitlán have eroded the lacustrine sediments of the mesa floor. From West (1964). By permission of the University of Texas Press.

Around Sabinas, Coahuila, there are sequences of coal and coral reefs of Middle Cretaceous age that further indicate locally emergent lands and warm-temperate to subtropical climates. By the end of the Cretaceous, the northern part of the Altiplanicie was mostly drained through continued uplift, while the southern part was still partly covered by shallow seas and lagoons bordered by coral reefs.

The geology of the Mesa Central (Fig. 2.2) is more complex than the Mesa del Norte and its geology is not well known. This is primarily because the relationships between existing structures, Late Cretaceous and Cenozoic plates, and pre-Jurassic plates are poorly understood. There is an equal uncertainty about the structural development of the Altiplanicie in relation to the uplift of the Sierra Madre Occidental and Sierra Madre Oriental. As noted, most of the region was receiving marine

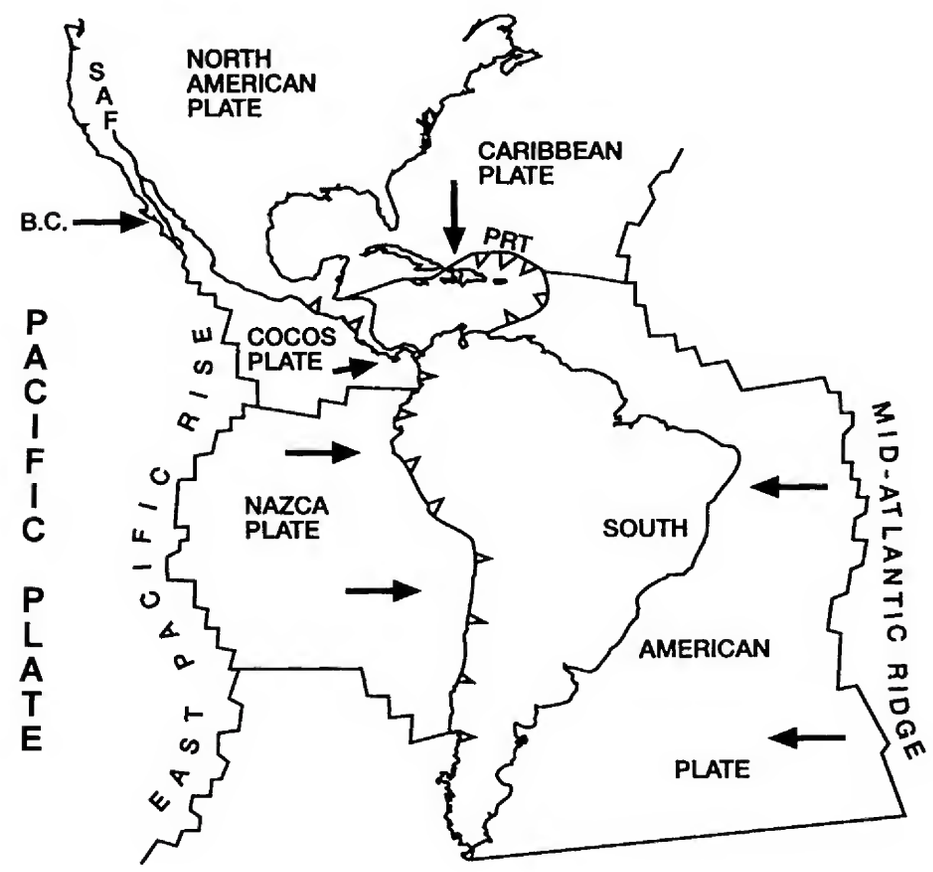


Figure 2.1. Index map of the principal plates and subduction zones affecting Latin America. B.C., Baja California; PRT, Puerto Rican Trench; SAF, San Andreas Fault. Arrows indicate direction of plate movement; open carets indicate trenches and direction of subduction.

sediments in the Cretaceous. In the Late Cretaceous, these sediments were locally faulted into horst and graben structures, intruded by volcanics, metamorphosed, and locally overturned. The central area was uplifted in the latest Cretaceous and Paleogene, which was somewhat later than in the north. In the Oligocene and Miocene, uplift associated with folding, faulting, and volcanism elevated hills of moderate elevation separated by numerous intervening valleys in the Mesa Central that continued to receive eroded clastic sediments throughout the middle and late Cenozoic (Nieto-Samaniego et al., 1999).

Sierra Madre Occidental (Fig. 1.6)—The Sierra Madre Occidental is the largest geologic province in Mexico. It is about 1300 km in length, averages 190 km in width, and is one of the world's largest volcanic fields (Ferrusquía-Villafranca, 1993). There was an initial period of intense orogeny between 100 and 45 Ma depositing the lower volcanic complex, another overlapping period between 54 and 34 Ma depositing the upper volcanic complex, and sporadic activity in later times. Thus, in the Middle and Late Cretaceous, there were emergent hills and low mountains along the axis of the present-day Sierra Madre Occidental. Emergent land is indicated by aquatic and terrestrial fossil plants of Maastrichtian age from the Olmos Formation near Nuevo Rosita in Coahuila. The origin of the western mountains is due to subduction of the Farallon Plate, abutment of the mainland against the East Pacific Rise, and the opening of the Gulf of California beginning ~34 Ma. These activities continue into Recent times as evident by the spectacular lava field of Volcán Ceboruco in Nayarit through which Mexico Highway 15 is cut (Fig. 2.3).

Sierra Madre Oriental—In a temporal sense the formation of the eastern mountains of Mexico parallels that of the Sierra Madre Occidental. The region was submerged in the Early Cretaceous and received sediments in moderately deep waters. These conditions are documented along the eastern slopes of the mountains by Cretaceous limestones exposed in Huasteca Canyon southwest of Monterrey in the Parque Nacional Cumbres de Monterrey, where marine rocks containing abundant ammonite fossils are spectacularly displayed (Fig. 2.4). Ammonites are indicative of moderate to deep marine

Figure 2.3. Lava flow from Volcán Ceboruco along Mexico Highway 15, Nayarit, Mexico.

Figure 2.4. Early to Middle Cretaceous limestones in Huasteca Canyon, Monterrey, Mexico. The beds contain ammonites indicating relatively deep-water deposition and are tilted from late Middle Cretaceous orogeny. Photograph by Shirley A. Graham.

water, and the canyon cuts through 305 m of exposed limestone. Uplift by compression forces from the east developed contemporaneously with the Laramide orogeny (Middle Cretaceous through the middle Eocene), during which the early Rocky Mountains of the western United States were forming. The compression forces were generated by spreading from the Mid-Atlantic Ridge while the west coast was held in place by the East Pacific Rise. Thus, there is a common mechanism for the uplift of the Sierra Madre Occidental, Sierra Madre Oriental, and the Altiplanicie during the Cretaceous and Early Tertiary. These three provinces have present-day geographic continuity with the Rocky Mountains and the Basin and Range Province of the United States, but the geologic relationships are not well understood (Drewes, 1978; Campos-Enriquez et al., 1999).

By the beginning of the Tertiary, the principal period of orogeny was over (Fig. 2.5). It was followed by emplacement of intrusive rocks in the late Eocene and subsequent peneplanation, some volcanic activity, and block faulting. The latter was particularly intense during the Pliocene, and together with volcanism, resulted in a rain shadow both to the east and west in the Altiplanicie (de Cserna, 1989). These orogenic events augmented dry conditions created by the location of the region under the descending arm of the Hadley circulation cell, continentality, and the middle Miocene drying resulting from ocean cooling by formation and calving of continental glaciers off Antarctica and the expansion of glaciation in the Arctic. The complex interaction between atmospheric circulation, orogenic events, and ocean cooling produced arid environments in the vicinity of 30°N. The biota responded through coalescence of pre-adapted and newly evolving types with the formation of the Sonoran and Chihuahuan desert vegetation. Although pre-adapted dry elements existed in North America as early as the middle Eocene, as shown in the Green River flora of Colorado–Utah (I: pp. 200–204), the coalescence of these elements began primarily in the middle Miocene, intensified in the Pliocene, and were shaped into communities of modern

Figure 2.5. Canyon of the Río Tula on the eastern slopes of the Sierra Madre Oriental south of Zimapan, Hidalgo, Mexico. The near-shore, horizontal Late Cretaceous/Paleocene limestones and sandstones were deposited after the period of principal uplift.

aspect during the warm-dry intervals of the interglacials.

Transvolcanic Belt—The Transvolcanic Belt is essentially a rugged, elevated, Cretaceous-basement plateau penetrated by late Cenozoic volcanic peaks. Average elevations are 2300 m in the east, 1600 m in the central part, and 1000 m in the west. Its origin was through uplift and volcanism generated by plate movement and subduction of the Cocos Plate beneath the North American Plate along the Middle American Trench (Fig. 2.1). There are a number of important basins in the region, including the Valley of Mexico where Mexico City is located. It initially began as an open basin draining to the south (Fries, 1960; Mooser, 1975) and closed at 0.78 Ma. Another is the Cuitzeo Basin system in central-western Mexico (Charo region, Michoacán; Israde-Alcantara & Garduño-Monroy, 1999). Its geologic development is instructive for interpreting vegetation and environmental history. Beginning in the late Miocene, volcanic and tectonic events altered paleodrainage into the basin. Faulting caused the formation of a shallow lake surrounded by extensive swamps. This was followed in the Pliocene by the development of a deep lake with a more restricted watershed and drier, well-drained habitats. In the Quaternary, block-tilting produced modern Lake Cuitzeo with conditions similar to its late Miocene origin. Thus, superimposed on global to regional climatic trends in precipitation, there were tectonic cycles generating moist, dry, and moist conditions that were "almost exclusively responsible for the development, evolution and obliteration of late Miocene–early Pleistocene lakes in the Charo region" (Israde-Alcantara & Garduño-Monroy, 1999, p. 225). These cycles complicate immensely the reconstruction of Quaternary vegetation in basin environments such as the Transvolcanic region (Chapter 4).

The rise of the Transvolcanic Belt began in the early Miocene (~23 Ma), and the high elevations developed primarily in middle to late Miocene (15 Ma) through Quaternary times. Their early history appears related to the upper volcanic complex of the Sierra Madre Occidental. Volcanism began in the western part and is probably related to the eastward movement of the Caribbean Plate. The famed peaks of Orizaba, Popocatépetl and Ixtaccíhuatl (Iztaccíhuatl; Fig. 2.6), Nevado de Toluca, Colima, Ajusco, and Volcán San Martín Tuxtla are part of the Transvolcanic Belt, and the region is the main center of earthquakes and volcanic activity in Mexico. Cone construction of Ixtaccíhuatl began before ~0.9 Ma (Nixon, 1989), and eruptions continue into the present (Palacios, 1996). The Volcán de Colima near the Pacific coast is the most active volcano in Mexico and is typical of those along continental margins adjacent to subduction zones (Rodríguez-Elizarrarás, 1995a, b). Three episodes of volcanic activity are evident in the lithostratigraphic units—the Nevado Group (middle to late Pleistocene); overlying avalanche deposits (10,000–4000 years B.P.); and andesite gravels and lahars (torrents of water-deposited volcanic debris) from the modern volcano (last 4000 years). There was an explosive eruption in 1913, and an Associated Press release for 9 June 2005 reports six recent eruptions.

Volcán de Paricutín in the state of Michoacán was intermittently active from February 1943 until March 1952, and after the first three years the vent had reached an elevation of 350 m above the original plain. The lava flows covered an area of 18.5 km^2 and destroyed the villages of Paricutín and San Juan Parangaricutiro (Foshag & González R., 1956). Mexico City was damaged by an earthquake of magnitude 7.8 on 19 September 1985, followed 36 hours later by another of magnitude 6.5. An estimated 10,000 people were killed and more than 200 public buildings were destroyed. The current volcanic activity of Popocatépetl (Palacios, 1996) to the east of Mexico City has been noted previously (Chapter 1, Mexico).

Balsas Depression—The Early and Middle Cretaceous rocks of the Balsas Depression are mostly marine and were deposited in a shallow to moderately deep sea that may have connected with the Gulf of Mexico and the epicontinental sea extending through central United States and Canada. These

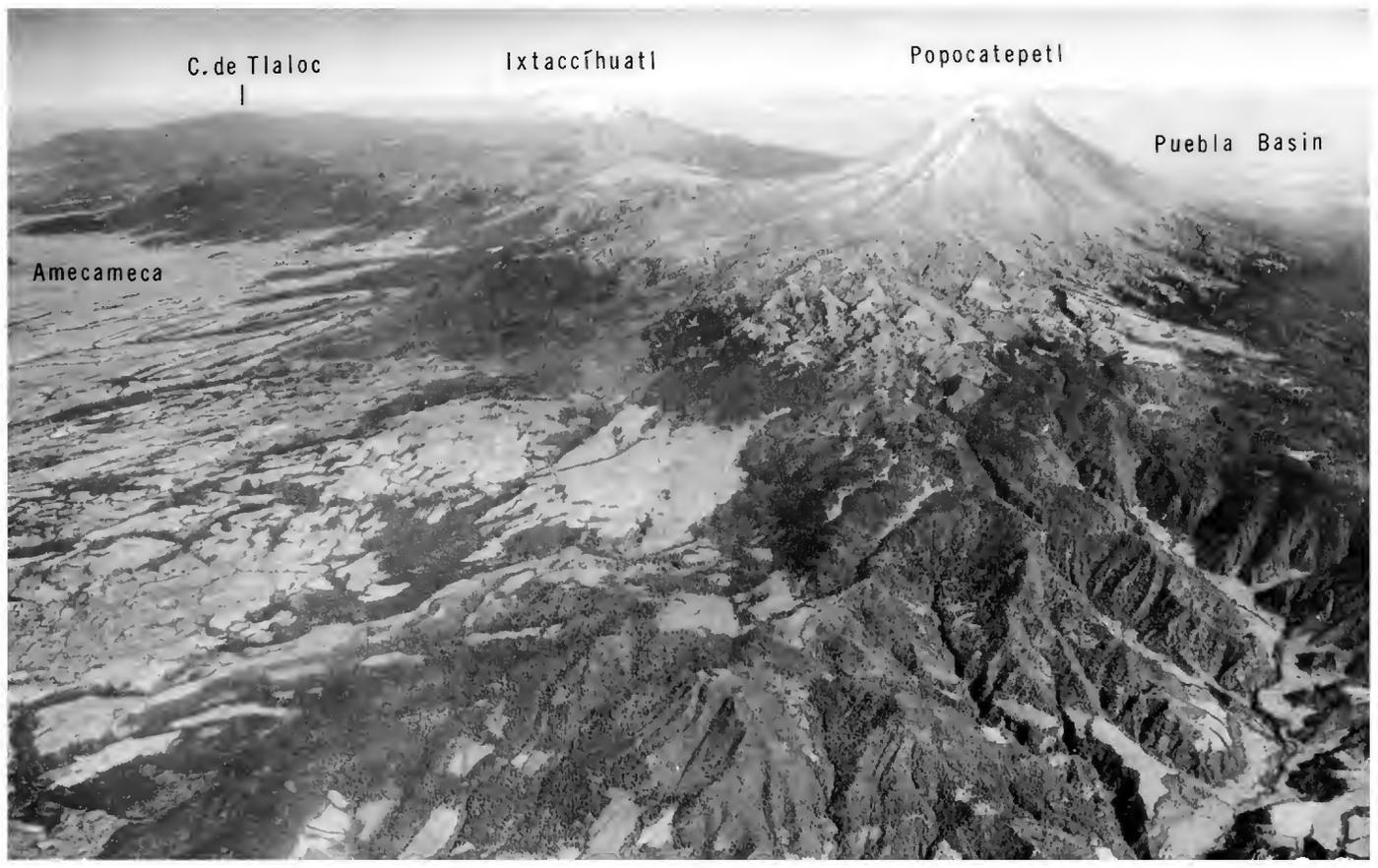


Figure 2.6. Volcanoes Ixtaccíhuatl and Popocatépetl and basins of the Transvolcanic Belt. From West (1964). By permission of the University of Texas Press.

waters regressed in the Late Cretaceous, and the basin began receiving sediments eroded from the bordering uplands. Tertiary strata are faulted fluvio-lacustrine (river and lake) deposits and volcanics.

Sierra Madre del Sur—These mountains border inland to the Middle American Trench that extends from about Las Tres Islas Marías (~22°N) to the Cocos Ridge (~9°N), 30–165 km offshore in the Pacific Ocean. The trench is where the Cocos Plate subducts beneath the North American Plate, currently at rates estimated as high as 6–7 cm/yr (Minster & Jordon, 1978; Nixon, 1982; Luhr et al., 1985). The region is rugged, it experiences numerous volcanic eruptions and earthquakes (7.8 M_S, 29 November 1978; Singh et al., 1980), and the geology is complex. The maximum elevation is 3703 m northwest of Acapulco and inland from the narrow Pacific Coastal Plain. It is possible that the Sierra Madre del Sur originated as an offshore island arc, like Baja California, and was accreted onto the mainland in the Middle and Late Cretaceous. The structural geology suggests uplift and drainage of the area in the Late Cretaceous and Paleogene. In rocks of middle Cenozoic age, there is evidence of magmatic activity associated with southward displacement of the Chortis Block in the Oligocene (Figs. 2.7, 2.16, 2.17; see below), and a change from compression to tension (stretching) forces, which created grabens and intensified volcanism in the Miocene (Morán-Zenteno et al., 1999).

Isthmus of Tehuantepec—Little can be said about the geology of the Isthmus of Tehuantepec relevant to Late Cretaceous and Cenozoic vegetation history except that it was submerged for much of the time. Given the plate movements in the Cretaceous through the early and middle Cenozoic and the magnitude of sea level fluctuations in the late Cenozoic (~121 m), parts of the isthmus probably were inundated frequently during this interval. A major fault system runs northward from near Salina Cruz–Tehuantepec on the Pacific coast and separates northern Mexico from a tectonic unit to the south called the Maya or Yucatán Block (Fig. 2.7). This block, initially located in the developing Gulf of Mexico, includes the region from southern Mexico to central Guatemala and was sutured onto southern Mexico along the Salina Cruz Fault during the Jurassic and Early Cretaceous.

Sierra Madre de Chiapas—The physiographic provinces of Chiapas have been described by Breedlove (1973, 1981), Ferrusquía-Villafranca (1993), and Frost and Langenheim (1974; Fig. 1.10). The region of the present Sierra Madre de Chiapas was covered by ocean for most of the Cretaceous. The waters were of varying depths, but shallows are indicated by the presence of coral reefs. The mountains have been compressed from the south into a series of plateaus (e.g., Meseta de San Cristóbal), depressions (Ixtapa), and cuestas with steep faces along which the principal rivers of Chiapas flow into the Pacific Ocean. The folding of these rocks into anticlinoria (hills) and synclinoria (valleys) occurred in early Miocene and later times (de Cserna, 1989).

East of the mountains is the Central Depression through which the Río Grijalva flows, and across which Mexico's largest dam has been built. The floor of the depression is covered with marine sediments of Cretaceous age and it was probably flooded throughout the Paleogene. Uplift then occurred as shown by an increase in terrigenous clastics and continental deposits. The area was drained by the end of the middle Miocene.

To the north and east are the Northern Front Ranges and High Plateaus. The limestone rocks of this province indicate that in the Late Cretaceous it was a shallow marine platform. Uplift occurred from the northeast in the middle and late Cenozoic. Volcanic activity also occurred during this time, in the Holocene (600, 1250, and 1700 years B.P.; Tilling et al., 1984), and continues to the present as evident by the eruption of El Chichón between 28 March and 4 April 1982. Fluctuations in sea level and orogeny resulted in frequent inundation of the low-lying regions during the Tertiary. The ancient shorelines run generally NW–SE and are marked by a series of lignites

and associated fine-grained mineral sediments paralleling the Front Ranges and High Plateaus, and are fully 90 km inland from the present Gulf Coast.

Yucatán Platform and Chicxulub Crater—

> "What minor evils might arise from the contact were points of elaborate question. The learned spoke of slight geological disturbances, of probable alterations in climate, and consequently in vegetation; of possible magnetic and electric influences. Many held that no visible or perceptible effect would in any manner be produced. While such discussions were going on, their subject gradually approached, growing larger in apparent diameter, and of a more brilliant luster. Mankind grew paler as it came. All human operations were suspended." (Edgar Allan Poe, "The Conversation of Eiros and Charmion," *Complete Stories and Poems of Edgar Allan Poe*, 1966, Doubleday, New York)

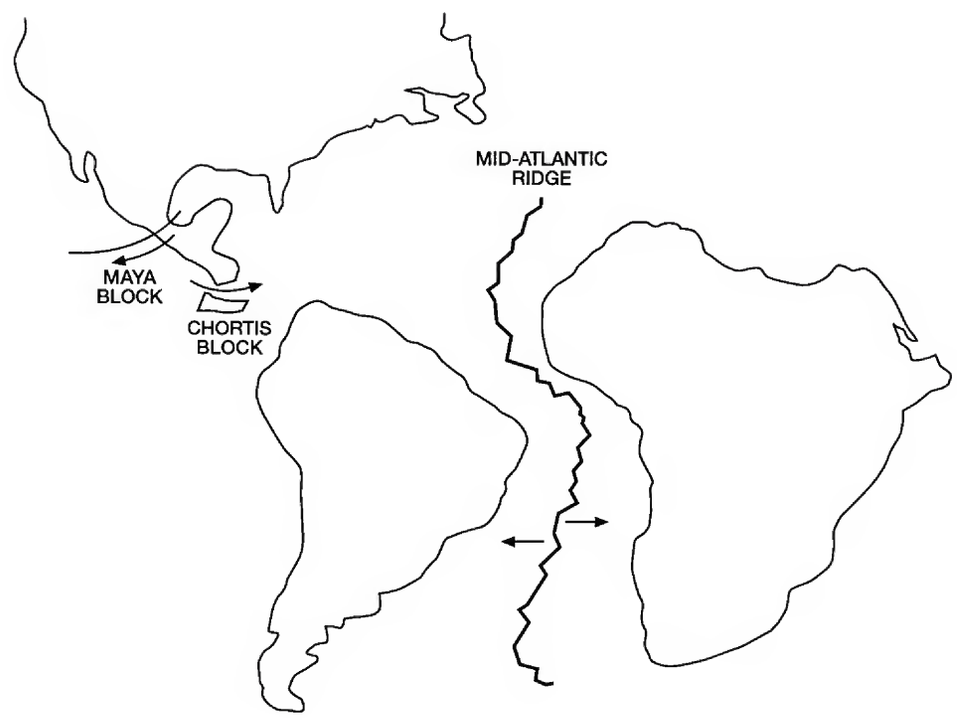


Figure 2.7. Index map showing the general positions of North America, South America, and the Maya (Yucatán) and Chortis blocks near the end of the Cretaceous.

Clearly one of the most spectacular events in Earth history was the impact of an asteroid 10 km in diameter on the northern coast of the Yucatán Peninsula near Chicxulub at the end of the Cretaceous (I: fig. 2.23; Fig. 2.8). It came from the southeast, traveling at an estimated speed of 90,000 km/hr, and it left a crater ~180 km in diameter now buried beneath 1–2 km of Tertiary carbonate rocks. The probable source was the breakup of the parent asteroid Baptistina (diameter ~170 km) at ~160 Ma (Bottke et al., 2007). The biological effects of the impact are not fully known for Latin America, where continuous fossiliferous sections across the K/T boundary are not as available as they are, for example, in the Raton Basin of New Mexico and Colorado in the United States (but see Vajda et al., 2001; Barreda et al., 2004; Vajda & McLoughlin, 2007), and now in the Denver Basin (see Dalton, 2007). There were certainly devastating consequences in the surrounding region because shocked (striated) quartz splashed out as far as Haiti, and a great tidal wave a kilometer or more in height left flood deposits near Tampico, Mexico, and Recife, Brazil.

During the Late Cretaceous, the Yucatán Platform was submerged (Cros et al., 1998). The rocks are mostly shallow marine limestones, and even today 95% of the peninsula is below 200 m in elevation. There was gradual emergence during the Cenozoic that left a sequence of Paleocene through Quaternary sediments eastward from the mountains of Chiapas, Mexico, and Guatemala. Coral reefs were present and still grow on the Caribbean side along the coast of Belize.

The long period of shallow submergence in subtropical waters created a setting ideal for the accumulation of abundant organic debris (kerogen). The oil expressed from the kerogen by heat and pressure generated by the overlying sediments accumulated in the porous limestone and sandstones of the Yucatán Platform. Faulting and abutment of the porous sediments against nonporous strata created stratigraphic traps in which the oil accumulated. Thus, the area is one of the richest petroleum preserves in Latin America. The Zona del Sur division of Petróleos de Mexicanos (PEMEX) is located at Coatzacoalcos in southern Veracruz and, because of the economic importance of the region, there is considerable information available on the geology. When lignites were being sought in our early projects as a relatively predictable source of plant microfossils, the location of these deposits and their stratigraphy in the vicinity of Coatzacoalcos was well known. The presence of UNAM's Tropical Biological Station at nearby Catemaco and the Flora of Veracruz Project also made this an exceptional setting for studies on vegetation history. Investigations continue with the Flora Mesoamericana Project, which includes the state of Chiapas, Yucatán Peninsula, and Central America (MO; UNAM; Natural History Museum, London; www.mobot.org/mobot/research/mesoamericaprojects.shtml).

Coastal Plains—In the Late Cretaceous and Early Tertiary, marine waters extended inland to the base of the developing Sierra Madre Oriental and through much of the Altiplanicie. In the middle Eocene the shoreline of the Gulf of Mexico was as far west as Nuevo Laredo as shown by fossils of shark, *Tarpon*, skates/rays, and pollen of the Asian mangrove palm *Nypa* in the Laredo Formation of south Texas (Westgate & Gee, 1990), and possibly *Nypa* pollen in deposits of the same age in the adjacent Burgos Basin of Mexico (Martínez-Hernández et al., 1980). Uplift drained the area, leaving a sequence of Late Cretaceous through Quaternary sediments at various places along the coast. The Late Tertiary and Quaternary deposits preserve a record of rapid changes in sea level, and movement of the land by orogenic and tectonic forces, as shown by an interfingering of marine and terrestrial facies. These regressive-transgressive events along the eastern passive margin of the Atlantic Coastal Plain are clearly reflected in the Pliocene formations around Coatzacoalcos in southern Veracruz where lignites containing *Rhizophora* pollen alternate with foraminifera-bearing marine sediments. In the Quaternary, a series of terraces was eroded

into the foreland of the Sierra Madre Oriental during times presumed to have been of "more or less constant tectonic uplift" (Ruiz Martínez & Werner, 1997). If so, the terraces reflect changes in sea level and could be correlated with global events and periods of climatic change, but further studies are pending. The Pacific Coastal Plain had a similar history, but it is more narrow along this active margin where the mountains are frequently close to the shore. In sections bordering the Sierra Madre del Sur, the plain is rising from continued subduction of the Pacific–Cocos Plate beneath Mexico.

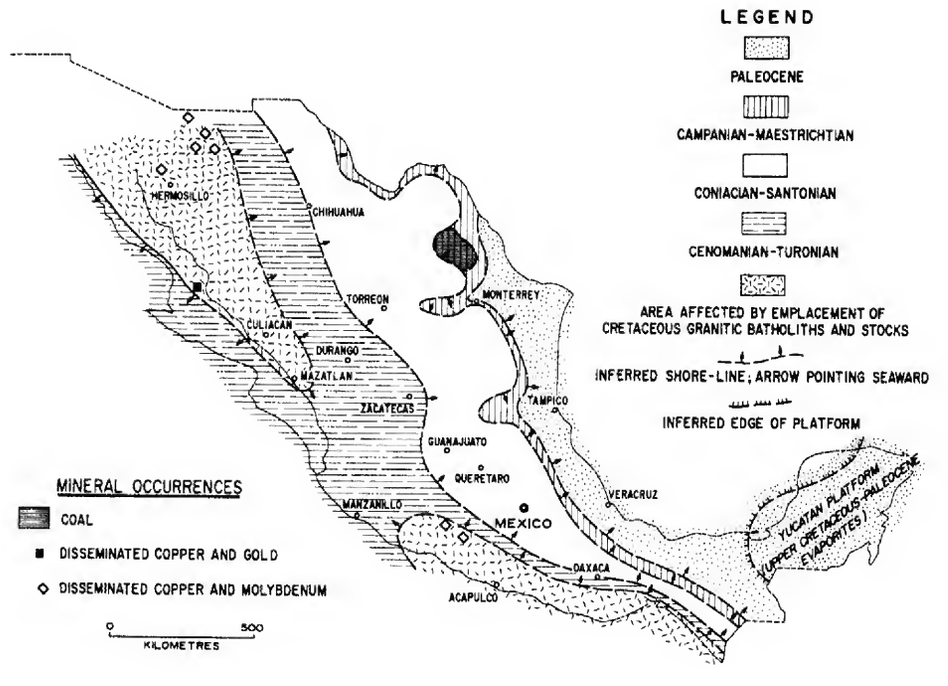


Figure 2.9. Late Cretaceous–Paleocene paleogeography of Mexico, showing the progressively eastward shifting shoreline with time. From de Cserna (1989). Courtesy of Geological Society of America.

Summary

One of the most relevant aspects of geology to vegetation history and historical biogeography is in revealing land-sea relationships. In the case of Mexico, the Late Cretaceous paleophysiography can be envisioned as a series of low to moderately elevated uplands along the axis of the present Sierra Madre Occidental and Sierra Madre Oriental with scattered offshore island arcs in the adjacent Pacific Ocean. These arcs included those later appressed to the mainland as modern-day Baja California and possibly the Sierra Madre del Sur. It should be noted, however, that studies of structural geology often are not as concerned with whether the various units were emergent or submergent as are biological studies that focus on reconstructing pathways of migration and other facets of terrestrial biotic history. Even so, it seems clear that much of the rest of Mexico, including the Yucatán Platform that moved from the developing Gulf of Mexico along the Salina Cruz–Tehuantepec Fault during the Jurassic and Early Cretaceous, Balsas Depression, Coastal Plains, Isthmus of Tehuantepec, and parts of the Altiplanicie, was covered by shallow to deeper marine waters (Fig. 2.9). The Sierra Madre Occidental and Sierra Madre Oriental extended toward the Rocky Mountain system with varying degrees of continuity and provided a discontinuous pathway for the movement of organisms to and from the northwest, through the Sierras and Altiplanicie of Mexico, eventually to the Transvolcanic Belt. In contrast, the Appalachian Mountains were mostly isolated from the uplands of Mexico by the epicontinental sea through the Cretaceous and early Paleocene. Migration overland for elements to and from the northeast into Mexico was more complex because it involved dispersal around the northern margin of the slowly retreating epicontinental sea.

Figure 2.8. Impact crater at Chicxulub, Yucatán Peninsula, Mexico. Upper white line is the northern Yucatán coast, dots along the southern margin of the crater are cenotes (sinkholes), and lower white line is the Ticul Fault. From Hildebrand et al. (1995), *Nature* 376. Reprinted with permission of Macmillan Publishers Ltd.

By the Early Tertiary, the sea had mostly disappeared from the interior, and other younger mountain systems, depressions, and coastal plains of changing width and elevation formed in the Middle Tertiary to create the modern landscape. This paleophysiography is relevant to the historical biogeography of Mexico because an increasing number of plant taxa presently restricted to East Asia, and previously known to have extended into the western United States during the Tertiary, followed these pathways into east-central Mexico (e.g., *Eucommia* in the Oligo–Miocene of Puebla). The orogenic and tectonic processes described still occur with dramatic consequences to shape the landforms of Mexico.

THE ANTILLES

The geology of the Antilles is important to understanding the vegetation history of the Americas because, along with Central America, they form the connecting links between the continents and between the hemispheres. Early studies on the geology of the Antilles include those for Jamaica (Sawkins, 1869), Cuba (Fernandez de Castro, 1884), Hispaniola (Gabb, 1873), Haiti (Butterlin, 1956, 1960), the Virgin Islands (Cleve, 1871), and the Lesser Antilles (Jukes-Brown & Harrison, 1891, 1892). An important summary of the geology of Cuba, Jamaica, and Puerto Rico was done by Robert T. Hill (1894 et seq.), whom Schuchert (1935) called "the father of Antillean geology" (Draper & Dengo, 1990). This summary was followed by Schuchert's own synthesis in 1935, which became the standard reference until modern times. Other important contributions were made by Richard Weyl (1961, 1966, 1980), who focused attention on the tectonics of the region. This aspect of Caribbean geology received further impetus from the first drilling operation in the deep ocean, which was on the Nicaraguan Rise (Emiliani, 1982), and which later was expanded into the Deep Sea Drilling Project (DSDP). The first DSDP site was in the Venezuelan Basin of the Caribbean Sea (Bader et al., 1970; Fig. 2.10) and the project continued as the Ocean Drilling Program (ODP) until September 2005, when the last site was drilled near Bermuda. The multinational effort is now called the International Ocean Drilling Program (IODP; see Ocean Drilling Stratigraphic Network [ODSN], http://www.odsn.de).

Modern geography—A myriad of small basins, ridges, troughs, plains, rivers, fans, aprons, and land fragments make up the topography of the Caribbean Basin (Fig. 2.10). They are the result of tectonic forces that began in the Middle Jurassic and continue to the present. To understand the origin of these structures, it is necessary to recall that as plates descend into the Earth's mantle at subduction zones along continental margins, the leading edge becomes molten at a depth of ~200 km. The lava may move to the surface along fissures (the Benioff Zone) to form a submerged or emergent offshore volcanic island arc. The trench on the ocean side of the subduction zone is called the fore-arc basin, while deep waters between the island arc and the continent or other existing landmasses form the back-arc basin. This is the setting that gave rise to islands that constituted the proto-Greater Antilles as North and South America moved apart in the late Mesozoic.

The Yucatán Basin is the back-arc or fore-arc basin of an ancient spreading center of Late Cretaceous to early Cenozoic age (Case et al., 1990). The Cayman Trough, about 1200 × 100 km in size, is likely of Miocene age. The Cayman Ridge is the site of active volcanism and is the only active spreading center in the Caribbean Basin (Holcombe et al., 1990). The upper Nicaraguan Rise and the Aves Ridge also may be remnants of Late Cretaceous and Early Tertiary spreading centers. The greatest depth in the Caribbean Sea is between the Cayman Ridge and the Nicaraguan Rise at 6800 m (the Bartlett Deep between Grand Cayman Island and Cuba). This is the second-greatest depth in the Atlantic Ocean next to the Puerto Rican Trench at 9200 m (Ladd et al., 1990).

The Grenada Basin separating the Aves Ridge from the Lesser Antilles island arc is a comparatively shallow structure, with depths of mostly less than 3000 m (Case et al., 1990). The time of its origin is unknown, but it is likely a back-arc basin of Cretaceous or Paleogene age resulting from the eastward movement of the Lesser Antilles subduction zone. The origin of the Colombian–Venezuelan Basin is not known, but it is either the result of a Late Cretaceous flood-basalt eruption (Donnelly et al., 1990b), or the site of a middle Mesozoic spreading center during the early separation of the North and South American plates (Meschede, 1998). The Aves Ridge with its single emergent peak, Aves Island, is a remnant arc of Cre-

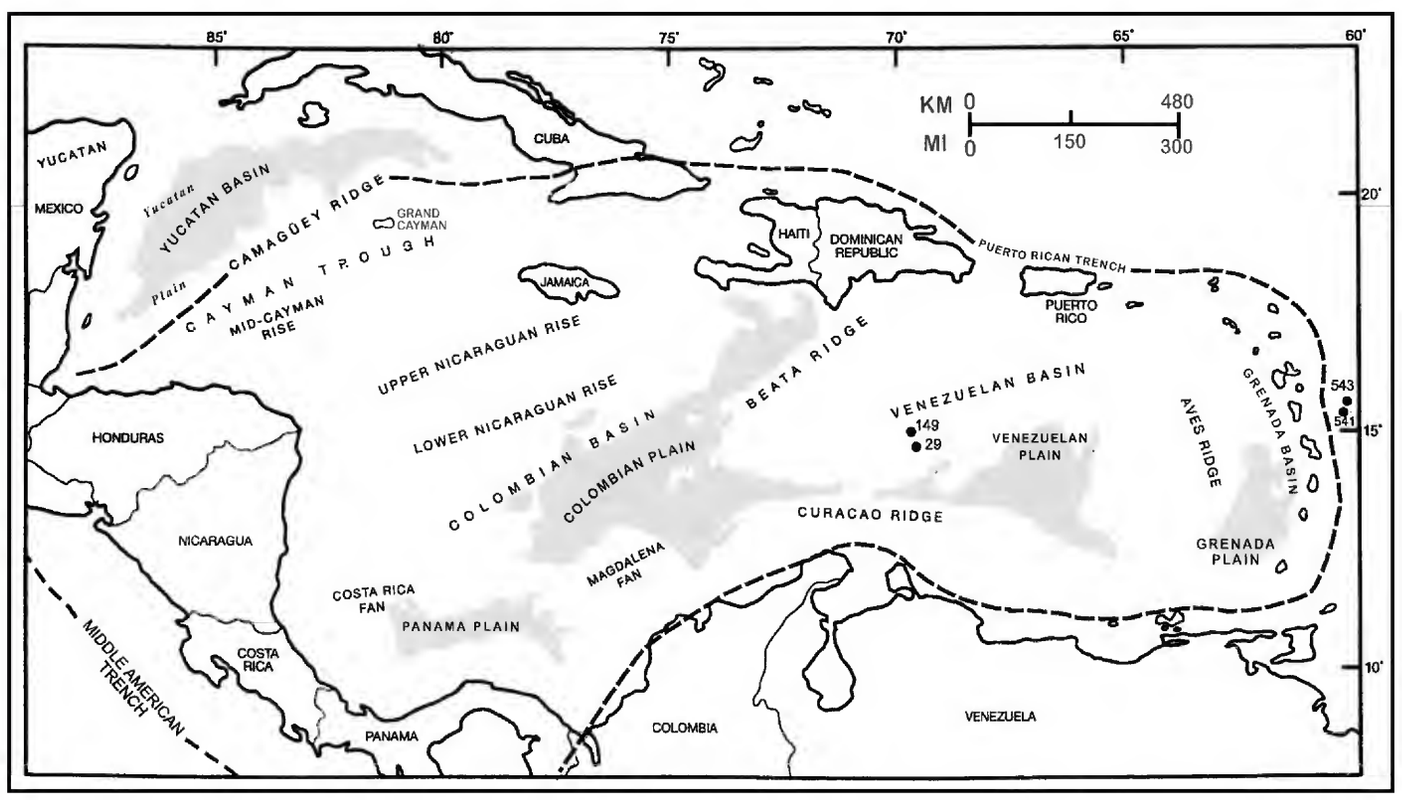


Figure 2.10. Index map of the structural features of the Caribbean Basin. Dots indicate Deep Sea Drilling Project sites.

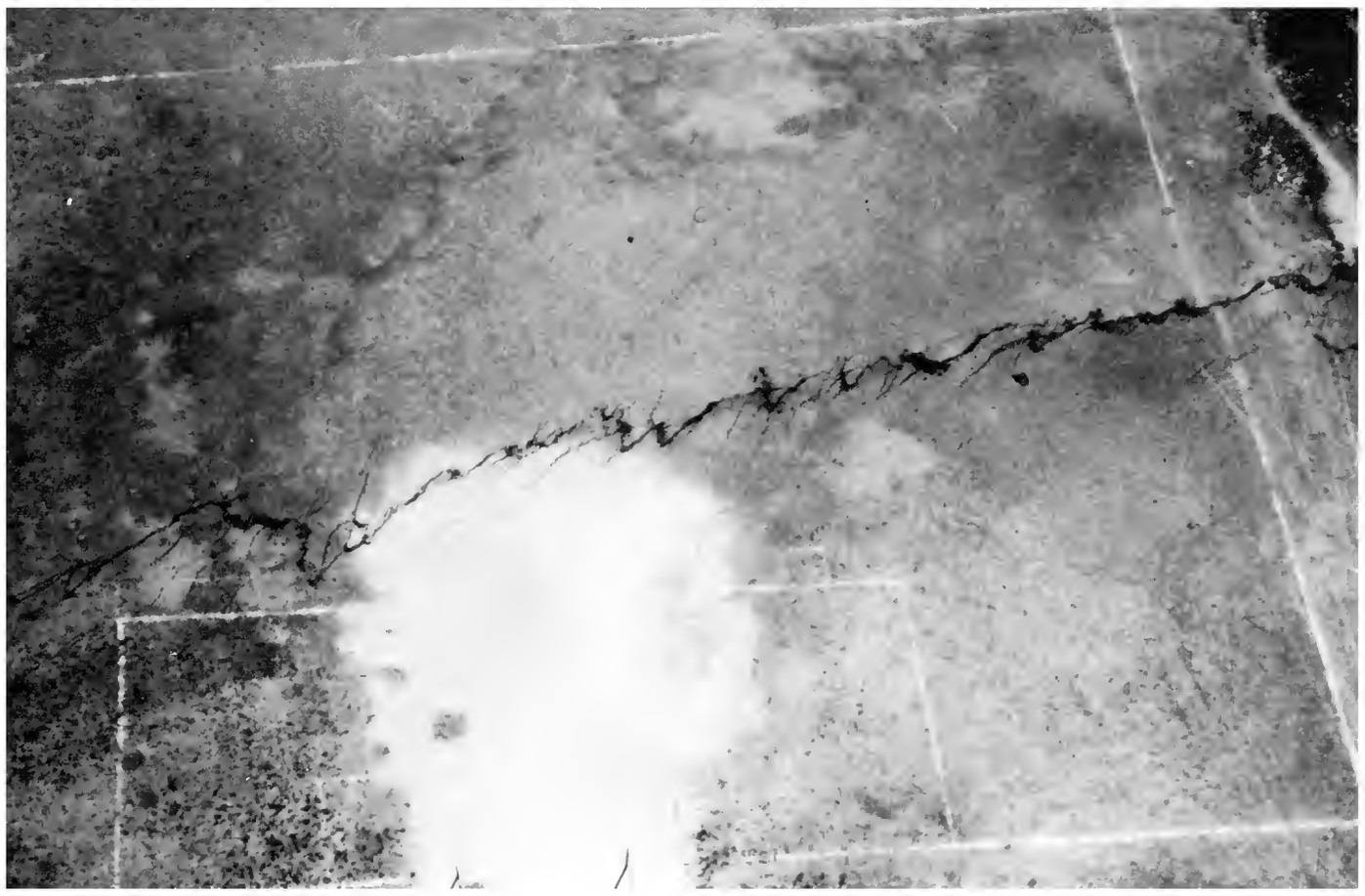


Figure 2.11. Motagua Fault across soccer field at Gualán, Guatemala, after the earthquake of 4 February 1976. Gualán is 25 km south of the west end of Lake Izabal. Note offset of the right white sideline of ~89 cm. From Plafker et al. (1976). Photograph courtesy of U.S. Geological Survey.

taceous to early Cenozoic age, and its emergent-submergent history has featured prominently in recent paleogeographic reconstructions linking South America with the Greater Antilles during the Eocene–Oligocene transition (see later section and Chapter 5).

The message that the physical features of the Caribbean Basin convey is that it is structurally complex and has had a complicated geologic history. Thus, simplified models that show land moving eastward from the vicinity of present-day Central America and then fragmenting into the modern Antilles do not provide an accurate physical context for reconstructing biogeographic events. Such models belie the related but intricate and individualized nature of the many subunits of the Caribbean Basin. The journalist H. L. Mencken is commonly credited for noting that "for every complex problem there is a solution that is simple, neat, and wrong." That is, if the intricacy of the solution does not match the complexity of the problem, it is often an over-simplification, and this has been the case with many of the early geologic models depicting the physical evolution of the Caribbean Basin.

Figure 2.12. Bent rails near Gualán, Guatemala, after the earthquake that took place on 4 February 1976. From Espinosa et al. (1976). Photograph courtesy of U.S. Geological Survey.

Definition of the Caribbean Plate—There is general agreement about the geographic definition of the Caribbean Plate (Fig. 2.10). The northwestern on-land boundary is the Polochic–Motagua Fault Zone across central Guatemala. Movement along this fault system produces the devastating earthquakes that characterize the region, including the one centered around El Progreso on 4 February 1976 (Plafker et al., 1976; Figs. 2.11–2.13). The boundary continues eastward as the Cayman Ridge or spreading center, a 100-km extension ridge 5–6 km deep at the contact between the North American and Caribbean plates. The boundary then crosses the Oriente part of Cuba and joins the Puerto Rican Trench along the northern border of the Greater Antilles. The trench is a subduction zone where the North American Plate dips under the Caribbean Plate. Dredging along the Yucatán Peninsula has revealed structural continuity between the peninsula and western and central Cuba, consistent with the generally accepted view that all three are part of the North

American Plate. There also are similarities between the geology of eastern Cuba, Hispaniola, Puerto Rico, Jamaica, the Nicaraguan Rise, Colombian Basin, Aves Ridge, Grenada Basin, the Cayman Trough, and other structures that are different from those uniting the Yucatán Peninsula and western-central Cuba. They are part of the Caribbean Plate.

The eastern boundary of the Caribbean Plate is along another subduction zone on the outer margin of the Lesser Antilles. Active volcanoes such as the Soufrière of Montserrat (Fig. 2.14) and Mt. Pelée on Martinique are part of the zone that constitutes the Lesser Antilles volcanic island arc of approximately late Eocene age. The eruption of Mt. Pelée on 8 May 1902 played a pivotal role in the subsequent economic and strategic history of the Caribbean region. The eruption took place the day before the U.S. Congress met to choose between Nicaragua and Panama as the site for the newly proposed interoceanic canal. The route through Nicaragua involved passage near the active volcanoes of that country and, with the devastation on Martinique so recent and vivid, the volcanically quiescent Panama was selected as the safer route.

The southern margin of the Caribbean Plate is the El Pilar, Oca, and associated faults of northern South America that join the Middle American Trench along the west coast of Central America (Fig. 2.15; Speed, 1985). The intersection of the Middle American Trench and the Polochic–Motagua Fault Zone is buried beneath Tertiary volcanics in western Guatemala (Guzmán-Speziale & Meneses-Rocha, 2000).

Time of origin—In addition to the definition of the Caribbean Plate, another point of general agreement is that the beginnings of the Caribbean Basin date to Middle Jurassic through Early Cretaceous times (200–165 Ma). Reconstructions place proto-Venezuela in the present Gulf of Mexico region adjacent to the southeastern United States, with the Maya (Yucatán) Block situated between the plates (Figs. 2.16, 2.17). This block moved westward early in the separation of the continents to its present position. The Yucatán Block, then the Chortis Block located along western Mexico, was sutured onto mainland Mexico in the Late Cretaceous. During the Jurassic and Early Cretaceous, North America and South America (with Africa adjoined) moved apart at a rate of ~5 cm/yr until ~130–120 Ma, creating a shallow sea in the present Gulf of Mexico–Caribbean region, as evident by evaporites of Jurassic age. New oceanic basalt was generated for the progressively widening basin and formed the early Caribbean Sea floor.

Figure 2.13. Movement of the Caribbean Plate (in the distance) eastward relative to the North American Plate (foreground) as shown by displacement of the white highway line at the bridge. Photograph by Shirley A. Graham.

Beyond these encouraging points of consensus on the structure, definition, and time of origin of the basin, there has been little further agreement until recently. One point of debate is the nature of the early sea floor in the Caribbean Basin. Meschede and Frisch (1998, 2002) suggest that the Venezuelan Basin is a remnant of an ancient spreading center that was the source of the basalts forming the new sea floor. They interpret paleomagnetic data as revealing a pattern of alignment of magnetite particles paralleling the basin that point to a near-American position for the early Caribbean Plate. If so, the Caribbean Plate developed between North and South America, and the islands of the Antilles formed close to their present position. Donnelly (1985, p. 92) believes that the reported magnetic lineations in the Venezuelan and Colombian basins cannot be sea-floor-spreading lineations because these basins are underlain by a Late Cretaceous flood basalt that overlies and obscures earlier spreading events.

Another suggestion as to the origin of the basin floor is that the basalts came from a hot spot in the Pacific Ocean. Hot spots are fissures in the Earth's crust through which molten material may move to the surface. Fissures may be located beneath continents and produce the kind of volcanic activ-

Figure 2.14. Soufrière Hills of Montserrat, ~1000 m. The most recent activity was an eruption on 28 July 2008. From Beard (1949). Used with permission of Oxford Forestry Institute.

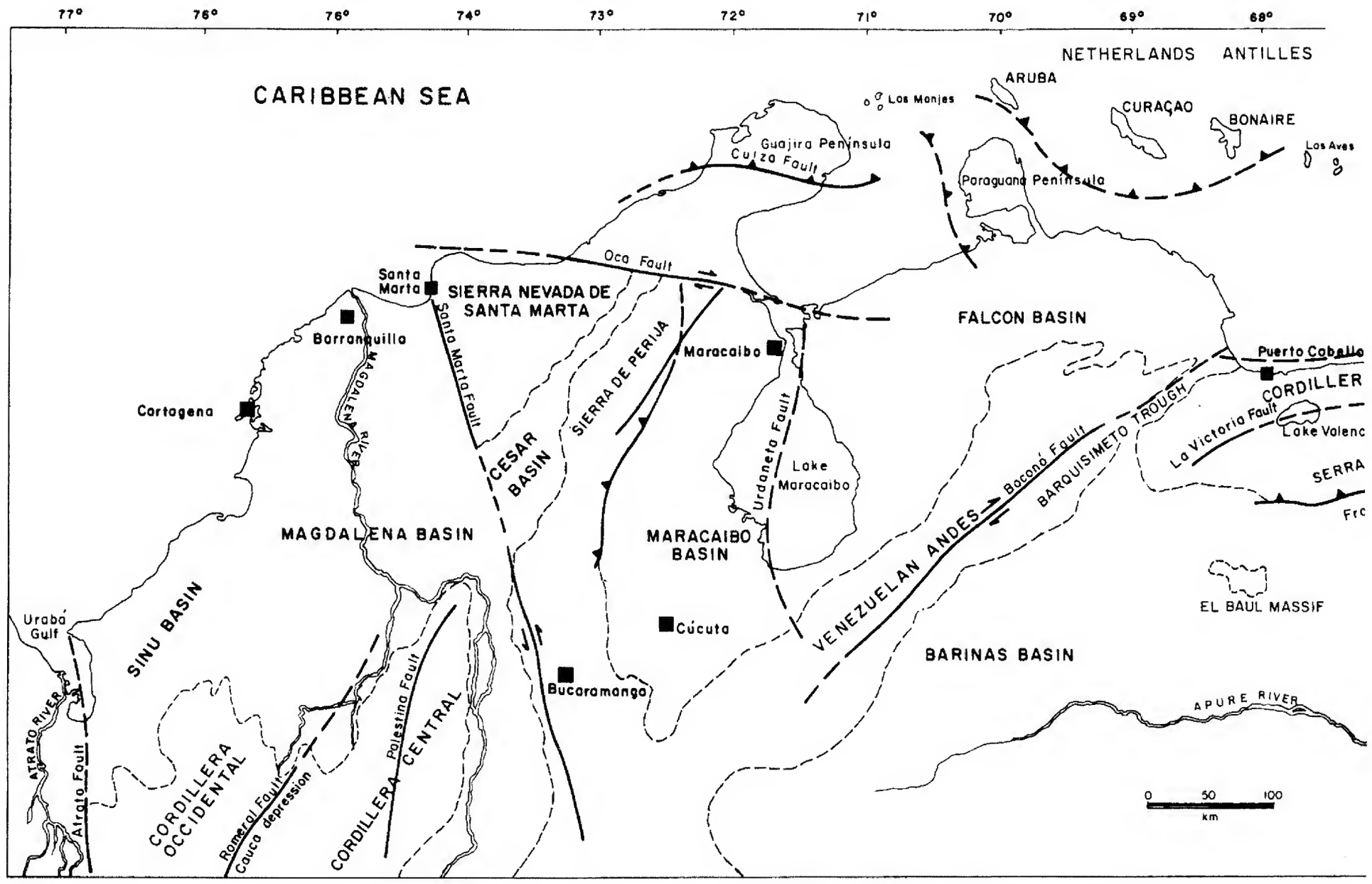


Figure 2.15. Southern boundary of the Caribbean Plate and nappe structures across northern South America. From Bellizzia and Dengo (1990). Courtesy of Geological Society of America. *(Continued on next page.)*

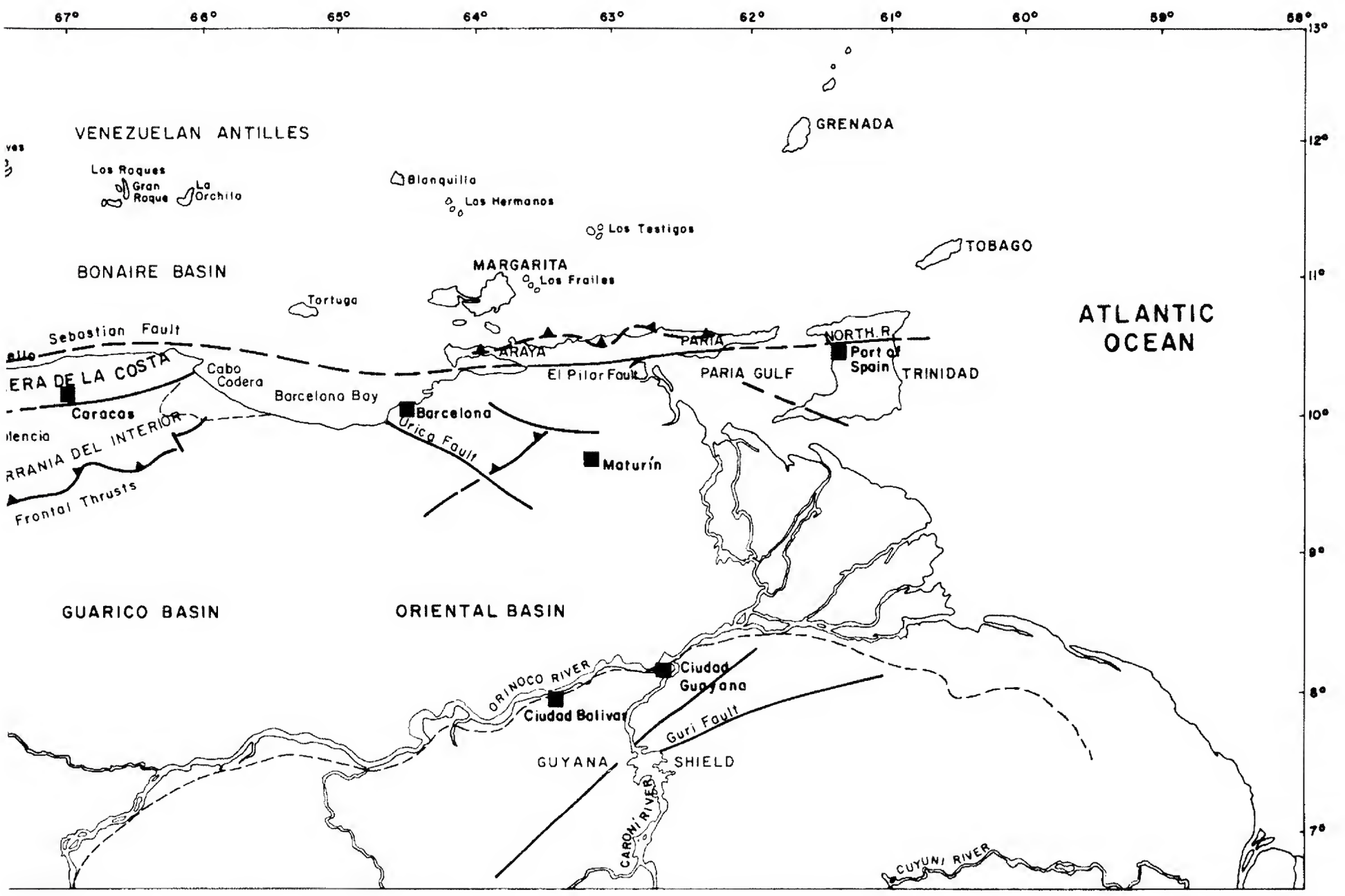
ity evident at Yellowstone National Park, Wyoming. They are found also under ocean basins, and the lava may emerge as islands, such as the Hawaiian Islands in the Pacific Ocean. The Galápagos Islands are located above a hot spot, and it has been suggested that this was the source of the basalts that formed the sea floor of the Caribbean Basin (Duncan & Hargraves, 1984; Hauff et al., 1997; Sinton et al., 1997). Meschede (1998; Meschede et al., 2002) believes this is unlikely because the basin began its development in the Middle Jurassic (~175 Ma), while the Galápagos hot spot did not form until the Oligocene to early Miocene (15–20 Ma; Christe et al., 1992). However, Hauff et al. (1997) argue for a Middle Cretaceous origin that would make the plume of the Galápagos hot spot a candidate for a source of flooring for the gradually opening Caribbean Basin. At present, the source of the original Caribbean Sea floor is unsettled.

More directly relevant to issues of biogeography is the history of the land fragments that either formed in the basin or were transported in from elsewhere. Two important components of this history are (1) the time and direction of movements, collisions, and separations, and (2) emergent-submergent events. After more than 100 years of study, most modern authors acknowledge that a satisfactory synthesis of the Late Cretaceous and Cenozoic geologic history of the Antilles is just being formulated. It is a daunting task because the Caribbean Basin is one of the most geologically complex regions in the world and many aspects of its tectonic history are still poorly understood. In the foreword to *The Geology of North America*, Case and Dengo noted (1990, p. x) that as of 1990:

> "Students and others unfamiliar with the region should remember that virtually every chapter would have had a different set of interpretative conclusions if a different set of authors had been selected. It has been said that a new model for the tectonic evolution of the region has been formulated by each new worker in the region."

A similar opinion was expressed by Donnelly (1989b, p. 110) with reference to the biological implications of the geological uncertainties:

> "Caribbean biogeographers have recently 'discovered' Caribbean geology. But whose geology have they discovered? Few of the…biological-geological syntheses that have been published recently [through the late 1980s] reflect the flavor of the controversy that dominates almost all aspects of the historical geological synthesis that is slowly and painfully emerging."



A complicating factor is that the Caribbean Plate is composed of several microplates with associated land fragments that have related but not identical migrational and emergent-submergent histories. They have moved somewhat independently, both vertically and horizontally, as a result of spreading center activity, subduction zone activity, and compression-extension forces exerted by the changing positions of the North and South American plates. A general impression of these movements can be gained from Web page images currently being developed. One is by C. R. Scotese (PALEOMAP Project Web site, http://www.scotese.com; see also *Science*, vol. 284, 1999, p. 1887), and another is by J. Pindell on the Caribbean Geology and Tectonics Web site (http://www.fiu.edu/orgs/caribgeol; see geological information on the Caribbean/tectonic reconstructions). Other aspects of Caribbean geology are discussed in Jackson (2002).

In assessing the various models that have been proposed, it is useful to keep in mind that both absolute and relative movements are involved in the positioning of plates. Absolute movement is defined in relation to the crust, while relative movement is defined in relation to adjacent plates. The New World continents all are currently moving westward as new crustal material is generated from the Mid-Atlantic Ridge. Early estimates by the NUVEL-1A model were that the Caribbean Plate is moving westward at 1.8 cm/yr, North America is moving westward at 3.0 cm/yr, and South America is moving westward at 3.3 cm/yr (DeMets et al., 1990; Gordon et al., 1997; Meschede, 1998). By these estimates, the current positioning of the Caribbean Plate is slowly eastward relative to North and South America at 1.2 and 1.5 cm/yr, respectively. However, recent global positioning system (GPS) data indicate that movement of the Caribbean Plate relative to South America is significantly faster and closer to 2.0 cm/yr (Pindell et al., 1988; Dixon et al., 1998; Weber et al., 2001). A rate of 2.0 cm/yr since the middle Eocene (55 Ma) calculates to an offset of 1100 km.

The migrational and emergent-submergent histories of the land fragments are of particular interest to taxonomists and biogeographers and, as noted by Donnelly (1989b, p. 110), this has been one of the least settled aspects of Caribbean geology:

> "A large part of the problem is that geologists do not address some of the questions that biologists need for their analyses. To a geologist it is relatively unimportant if an island arc is broadly emergent or mainly submergent, whereas the biologist is vitally interested in that information. On the other hand, the movement of the 'Caribbean plate' eastward from putative Pacific location is a question close to

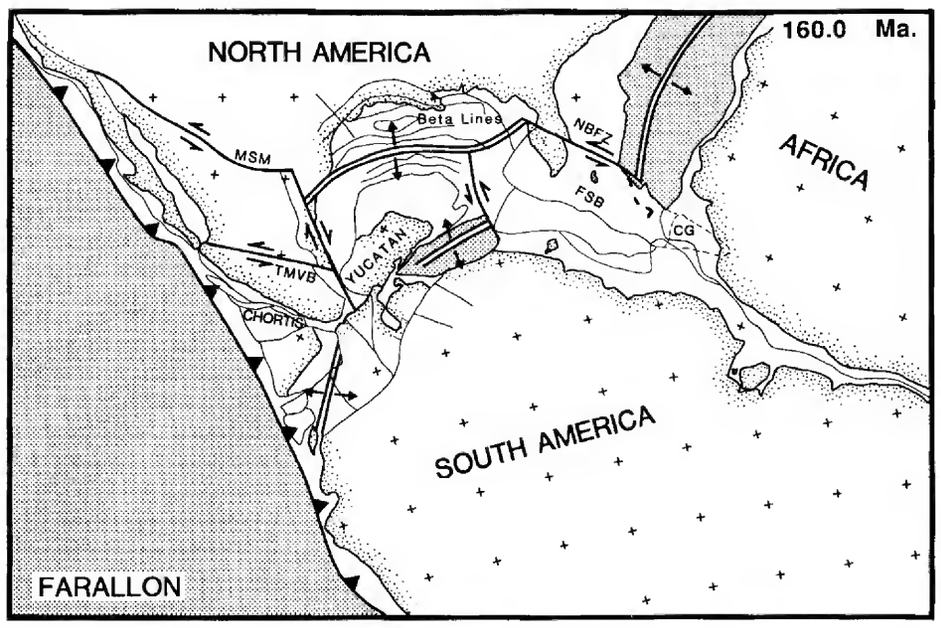


Figure 2.16. Tectonic reconstruction at 160 Ma (Cretaceous, Oxfordian). Reprinted from Ross and Scotese (1989), with permission of Elsevier Science Publishers, Amsterdam.

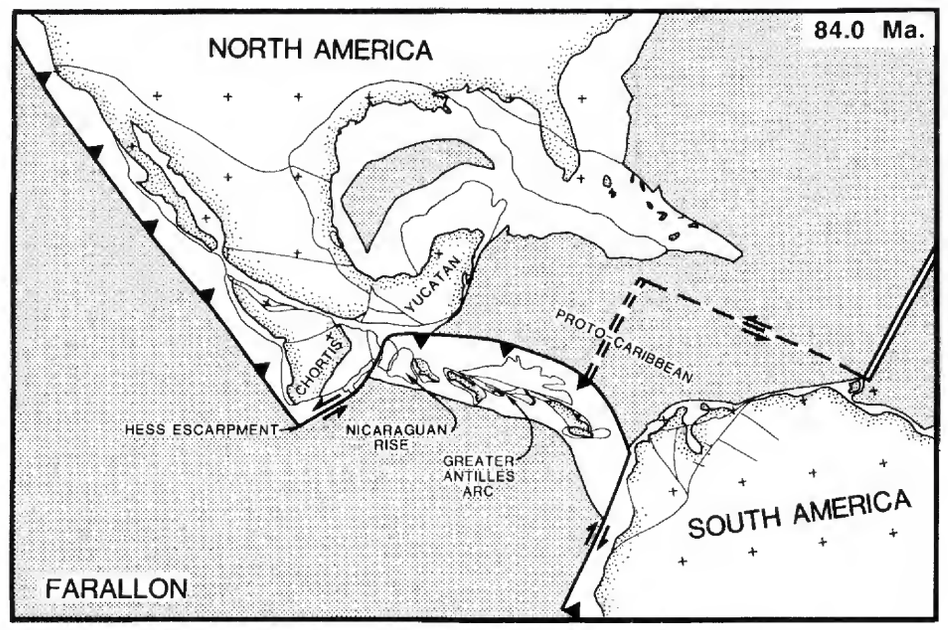


Figure 2.17. Tectonic reconstruction at 84 Ma (Cretaceous, middle Campanian). Reprinted from Ross and Scotese (1989), with permission of Elsevier Science Publishers, Amsterdam.

> the hearts of geologists, but probably of relatively little interest to biologists. A 'proto-Antillean arc' may be of value for biological purposes regardless of whether it occupies the position of present Central America or the present Antilles, as long as connections between North and South America are the major issue."

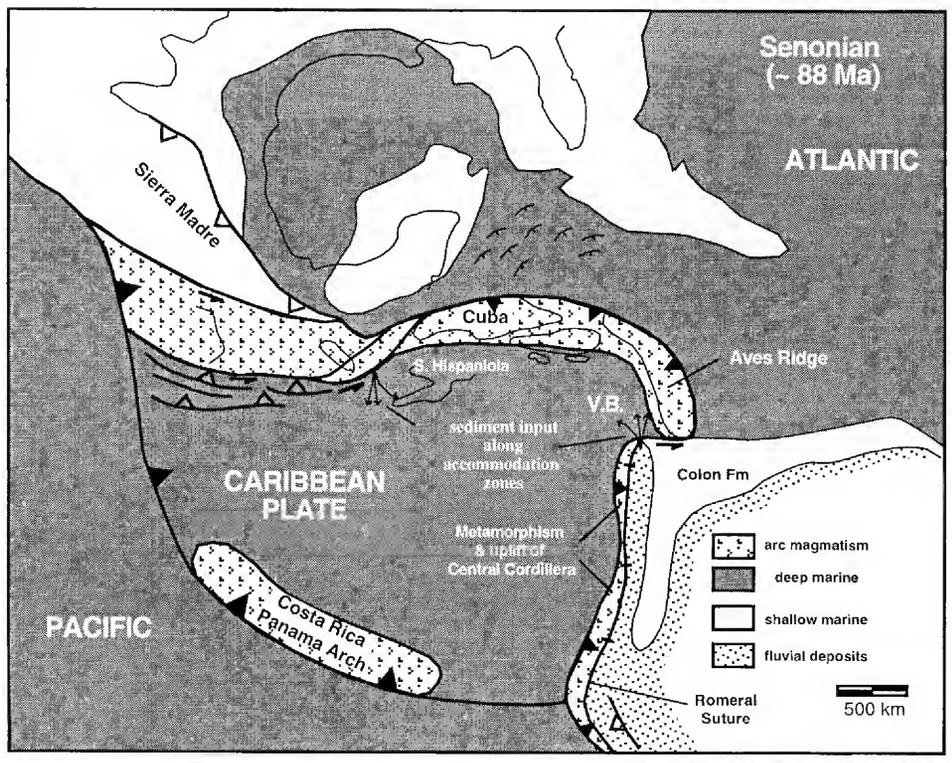
In order to follow the extensive and often confusing literature on the geologic history of the Caribbean region, the various models proposed to explain that history are grouped below into the following categories:

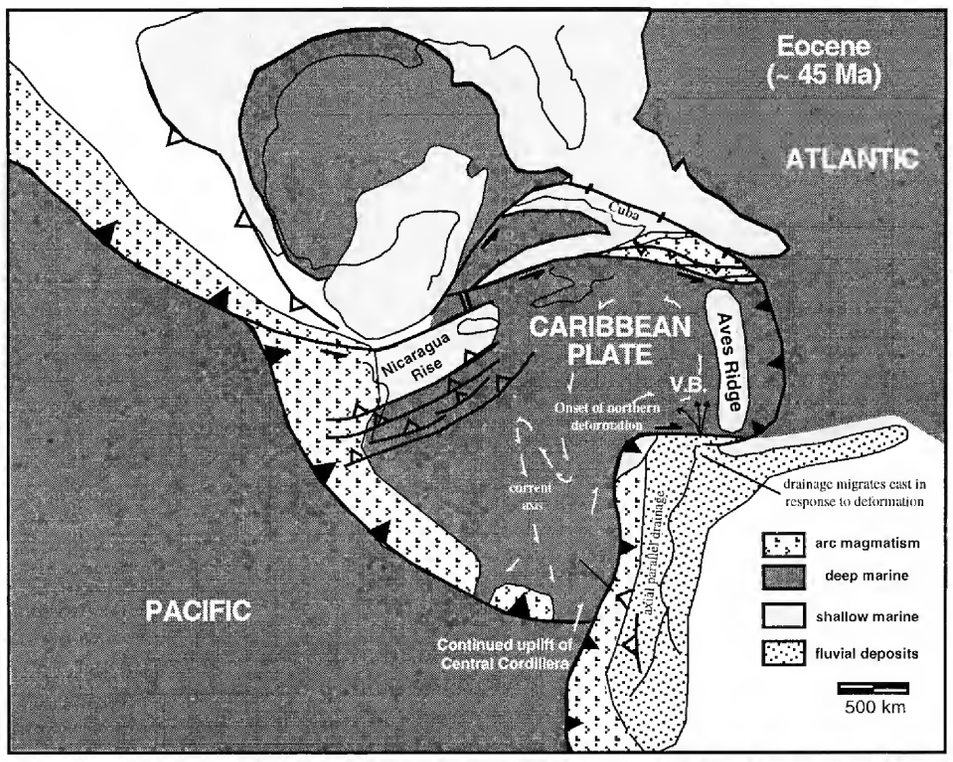
I. Fixist Models—the islands originated at or near their present position
   A. Plate tectonic events were not involved in their origin (e.g., Woodring, 1954; Weyl, 1966, 1973; Meyerhoff & Meyerhoff, 1972; Morris et al., 1990)
   B. Plate tectonic events were involved (Meschede & Frisch, 1998)

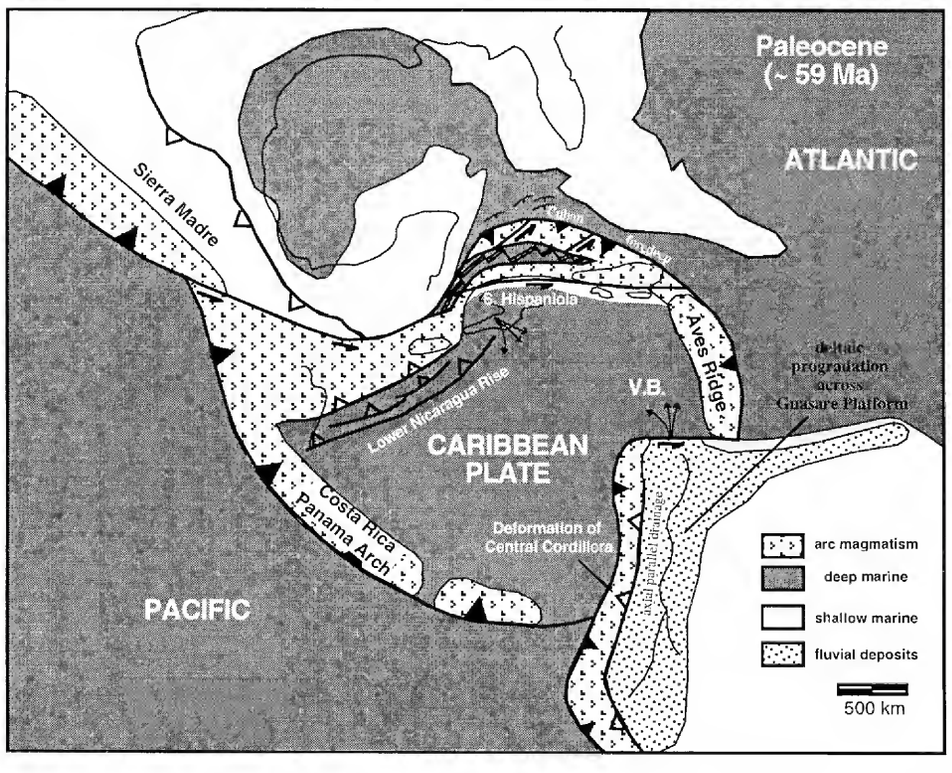
II. Mobilist Models—the islands originated elsewhere and were transported to their present position
   A. Minimalist—transported ~130 km from the vicinity of Yucatán–northern Central America (Burkart, 1978, 1983; Anderson et al., 1985; Donnelly et al., 1990a)
   B. Maximist—transported 1000 km or more from the vicinity of the present isthmian region (Hess & Maxwell, 1953; Freeland & Dietz, 1971; Malfait & Dinkelman, 1972; Wadge & Burke, 1983; Burke et al., 1984; Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent & Gahagan, 2002; Pindell & Barrett, 1990; Pindell, 1994)

Most students of Caribbean geology agree that plate tectonics were involved in its history and that relative eastward movement has occurred. The "fixist" view has given way to more recent discussions that focus on whether there was limited movement from near the present Yucatán Peninsula–northern Central America or more extensive movement from the eastern Pacific Ocean through the portal that was developing between North and South America. Those working with on-land expressions of the movement (viz., along the Polochic–Motagua Fault Zone across Guatemala) have argued for minimal movement, while those working offshore (viz., along the Cayman Trough) favor more extensive movement. According to Donnelly et al. (1990a, pp. 54–55):

> "The presence or absence of such motions has formed one of the most bitterly contested geologic questions in the entire Caribbean area. One school of thought is that these faults [Motagua–Polochic] are the extension of the southern boundary fault of the Cayman Trench (Taber, 1922), and have a collective Cenozoic offset of 1,000 km or more (Hess & Maxwell, 1953; Burke et al., 1984; Wadge & Burke, 1983).
>
> Most field geologists working in Guatemala have minimized the total Cenozoic offset on the major fault systems. The Polochic fault has received the most attention: Burkart (1978, 1983), Burkart and Moreno (1983), and Burkart and Self (1985) have all argued persuasively for about 130 km total offset. Anderson et al. (1985) challenged these estimates; they prefer a total offset of only 'several kilometers.' Most workers [investigating the on-land sites in Central America] favor the Burkart interpretation, and none favors a larger offset.







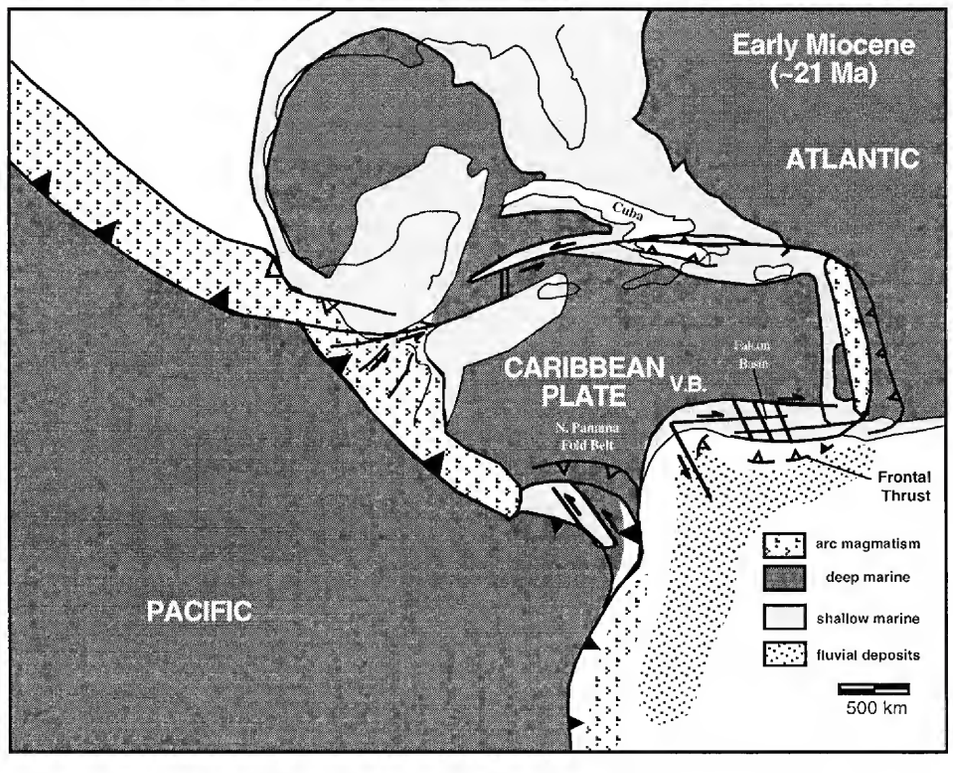


Figure 2.18. Plate reconstructions of the Caribbean during the Late Cretaceous (Santonian, ~88 Ma) and Early Tertiary (Paleocene, ~59 Ma). Reprinted from Driscoll and Diebold (1999), with permission of Elsevier Science Publishers, Amsterdam.

Figure 2.19. Plate reconstructions of the Caribbean during the Eocene (~45 Ma) and early Miocene (~21 Ma). Reprinted from Driscoll and Diebold (1999), with permission of Elsevier Science Publishers, Amsterdam.

> Several lines of evidence point to 130 km of offset on the Polochic fault system and perhaps no more than a few tens of kilometers on the Motagua system. The problem of accommodation of about 1,000 km sinistral Cenozoic offset in the Cayman Trough remains unresolved."

It is now being resolved, however, and among the two mobilist models, the maximist version is supported by an increasing amount of geological evidence. In this connection, Pindell (pers. comm., 2001) has noted that a difficulty in verifying the minimalist model is that if movement was more extensive, there would be no on-land markers remaining to measure it by because the greater offset (e.g., 1000–1200 km) is several times greater than all the exposed land area across Guatemala along the Motagua–Polochic Fault Zone.

There are many aspects of the history still to be resolved, and several are important to biology. Pindell and Barrett (1990) list 13 variations of the maximist model, but there has been recent convergence toward the version of Pindell (1994; Pindell & Barrett, 1990; Mann, 1999; Mann, pers. comm., 2001), and it is the one adapted here as a basis for discussing Caribbean vegetational history.

The earlier versions of the maximist model (e.g., Malfait & Dinkleman, 1972) show an arc of continuous or nearly continuous land connecting or nearly connecting the North and South American continents through the isthmian region. Later this land fragmented, the pieces moved eastward, and they formed the islands of the Greater Antilles. Among the many implications of this history is that it provides a physical basis for the contention that vicariance was a principal basis for distribution and speciation mechanisms in the Caribbean. The model of Pindell and Barrett (1990; Pindell, 1994) proposes a different history that implies a greater role for dispersal.

The plate tectonic model of Pindell and Barrett (1990; Pindell, 1994) places the origin of the Caribbean Plate and the Greater Antilles in the eastern Pacific Ocean, adjacent to the separating North and South American continents, during the Early Cretaceous (Valanginian, ~130 Ma). This early volcanic island arc was mostly submerged, although there is a report of land plants from the Early Cretaceous of Hispaniola (Neocomian, ~145–130 Ma; from Smiley cited in Kesler et al., 1991; Smiley, 2002; Iturralde-Vinent & MacPhee, 1999, p. 19). Other parts of the basin now submerged may also have been briefly emergent as separate islands; e.g., the Cayman Ridge, Nicaraguan Rise, and Aves Ridge (Perfit & Williams, 1989). In this connection, it is noted that sea level in the Late Cretaceous was up to 300 m higher than at present. Also, the early terrestrial deposits of the Antilles are overlain by later deposits of Albian age (~112–97 Ma) that are marine. From the Late Cretaceous period to the late Cenozoic, there is no clear geologic evidence that North America and South America were connected or nearly connected by continuous land or extensive emergent islands (Figs. 2.18, 2.19).

The Caribbean Plate achieved an easterly position vis-à-vis the two continents by relative movement. The leading edge began colliding obliquely (transpression) with the stable Jurassic–Late Cretaceous Bahamas Platform during the Late Cretaceous and in the late Paleocene and earliest Eocene (59–56 Ma). Fragments of northern–western–central Cuba were already in place and were followed progressively to the east by fragments that would eventually constitute eastern Cuba (Sierra Maestra Block), Hispaniola, and Puerto Rico (Gordon et al., 1997). As noted previously, during this transport, between ~130 and 56 Ma, there were likely intervals of emergence and submergence, but sustained emergence probably began with the compression of the island arc against the Bahamas Platform in the middle Eocene (45–49 Ma). According to Iturralde-Vinent and MacPhee (1999, p. 3): "the existing Greater Antillean islands, as islands, are no older than middle Eocene. Earlier islands may have existed, but it is not likely that they remained as such (e.g., as subaerial entities) due to repeated transgression, subsidence, and (not incidentally) the K/T bolide impact and associated mega-tsunamis. Accordingly, we infer that the on-island lineages forming the existing Antillean fauna [and flora] must all be younger than the middle Eocene."

Some further details can be added for individual islands of the Antilles based on regional studies.

Cuba—Running southwest to northeast across Cuba is the Pinar Fault Zone. North and west of the zone, the rocks represent part of the original volcanic Cretaceous island arc. This part was in place and appressed against the Jurassic to Late Cretaceous Bahamas Platform (Draper & Barros, 1994), prior to the arrival of other fragments in the late Paleocene–early Eocene (Gordon et al., 1997). Another fault, the Cauto Fault Zone, runs between central and eastern Cuba through the Cauto Basin. It may represent the contact where eastern Cuba (plus northern Hispaniola and Puerto Rico) was added to central and western Cuba in the early to middle Eocene

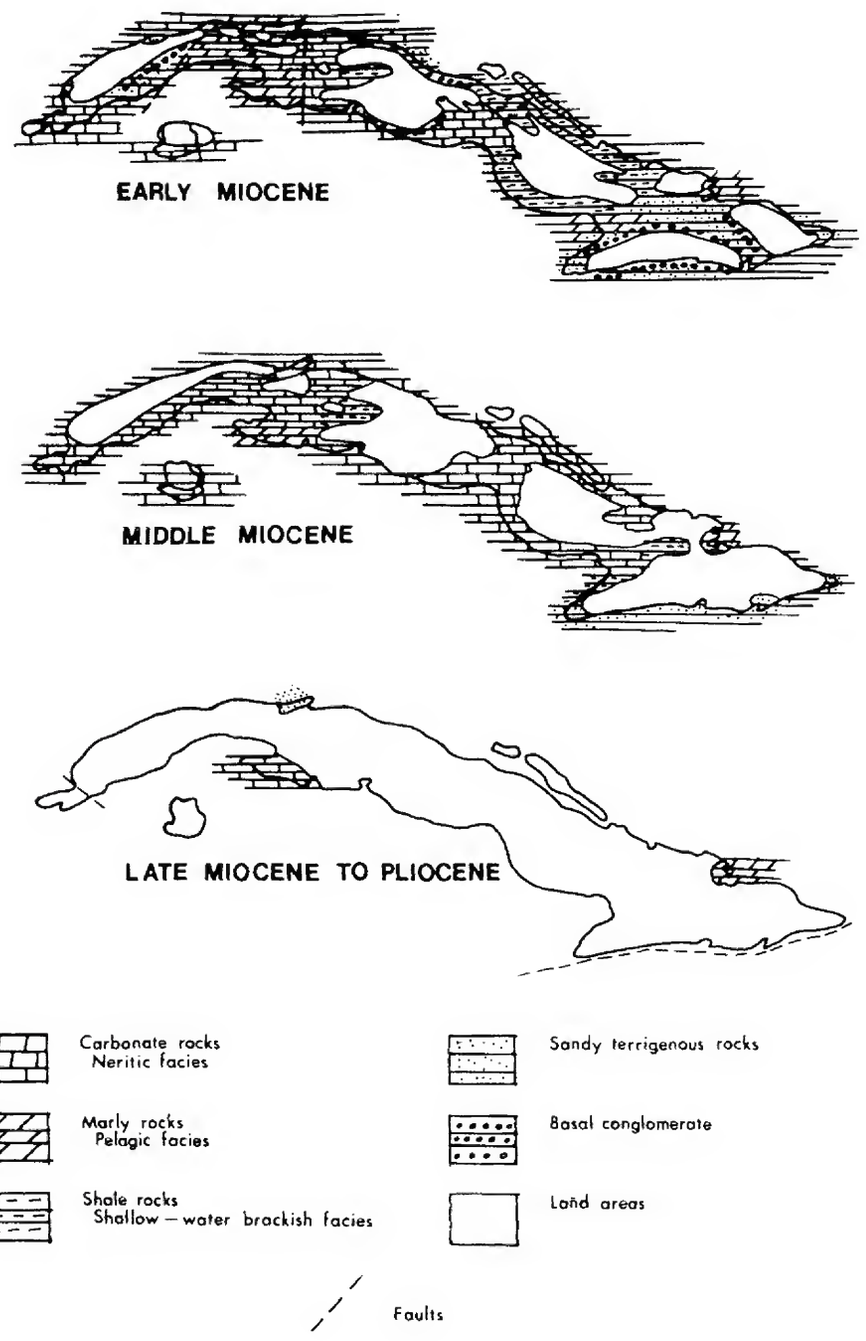


Figure 2.20. Miocene and Pliocene paleogeography of Cuba. From Lewis and Draper (1990), based on Iturralde-Vinent (1969). Courtesy of the Geological Society of America.

(another interpretation is that eastern Cuba was already part of the island by the Paleocene [James Pindell, pers. comm., 2001]). When proto-Cuba began colliding with the Bahamas Platform, the curvature of the platform caused the western and central part to slow first, while the eastern part moved along the Cauto Fault Zone with continued eastward drift of the Caribbean Plate. Full dry land contact between the various fragments of Cuba was achieved in the late Miocene with disappearance of the Havana–Matanzas Channel (Iturralde-Vinent & MacPhee, 1999, p. 35; Fig. 2.20). The island has had an immensely complex geologic history, however, and as noted by Donnelly (pers. comm., 2001), "it is likely composed additionally of fragments assembled in the early Cenozoic that included everything from fragments of the Chortis Block to the Bahamas Platform, including the newly formed ocean crust of the Yucatán Basin." The opening of the Yucatán Basin (Late Cretaceous to Eocene) may have been a driving force in pushing a series of land fragments against the Bahamas Platform that were amalgamated into the northern parts of western and central Cuba. The principal periods of uplift and deformation on Cuba were in the Late Cretaceous and Paleocene between 66 and 54 Ma (collision of the original volcanic island arc with

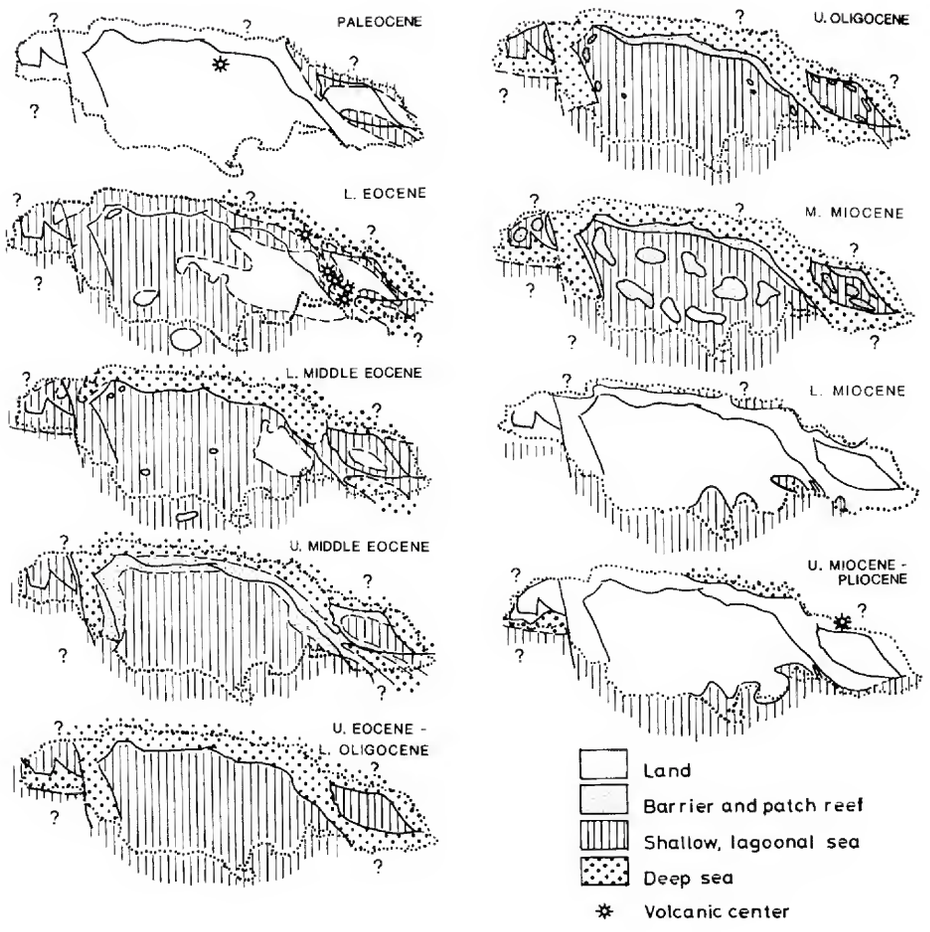


Figure 2.21. Paleogeographic maps showing the Tertiary evolution of Jamaica. From Lewis and Draper (1990), based on Eva and McFarlane (1985). Courtesy of the Geological Society of America.

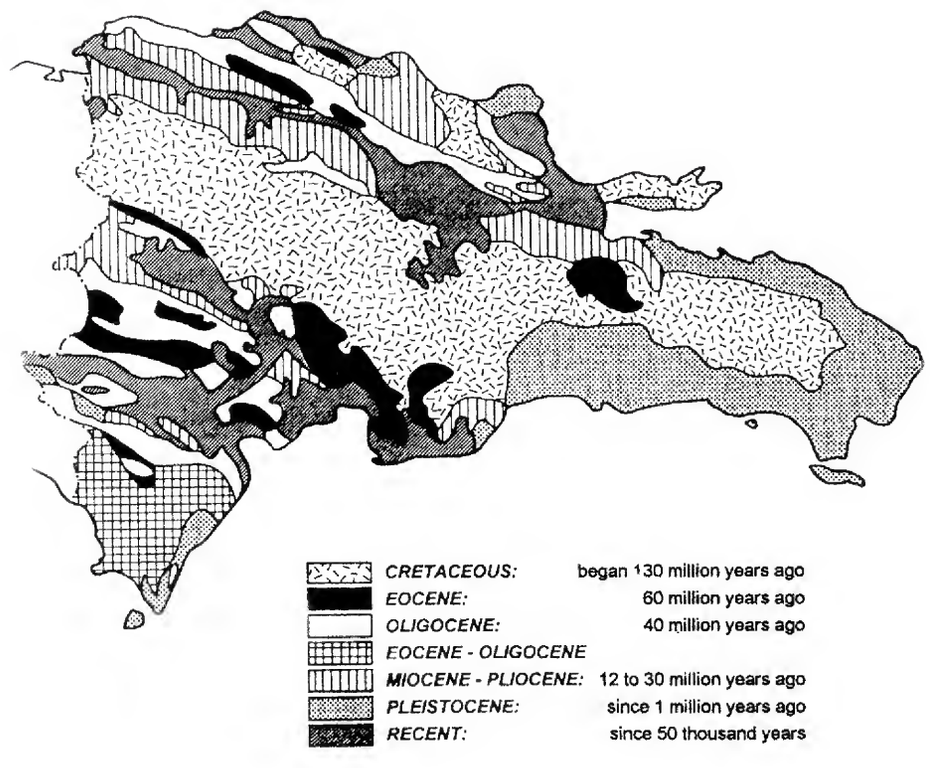


Figure 2.22. Geologic map of the Dominican Republic. The Cordillera Central (D.R.)–Massif du Nord (Haiti) is the zone of Cretaceous crystalline rocks across the center of the island. From Bolay (1997) based on Nuñez Molina (1980). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

the Bahamas Platform). Emergence began mainly in the middle Eocene between 44 and 47 Ma with continued compression and the arrival of other fragments (Lewis & Draper, 1990, p. 92). Almost all of Cuba was emergent, in its present position, and of essentially modern configuration by the late Miocene (19–12 Ma; Fig. 2.20). In the Quaternary, periodic lowering of sea level by ~120 m at the glacial maxima connected the shallow seas bordering Cuba into expanded mangrove and other swamp habitats. The Mapa Geológico de Cuba (1990) illustrates the age and types of rocks that outcrop on the island.

Jamaica—The island of Jamaica was a prominent site for early studies on Caribbean geology. The British geologist Henry Thomas de la Beche visited family estates on the island between 1823 and 1825 and prepared a geologic map of eastern Jamaica (de la Beche, 1827). This is likely the first geologic map for the Western Hemisphere and, following William "Strata" Smith, he attempted to show formations and ages rather than just rock types. De la Beche later established and served as the first director of the British Geological Survey, the first geological survey in the world.

The geologic evolution of Jamaica, like that of the other islands of the Greater Antilles, began in the Cretaceous as part of the Antillean island arc system. Volcanic and metamorphic rocks of the Blue Mountains in the east are the oldest on Jamaica and are Campanian to Maastrichtian in age.

An aspect of Jamaican geology that is of special interest for vegetation history is that there are few rocks of terrestrial origin known from the middle Eocene to the late Miocene (Lewis & Draper, 1990; Fig. 2.21). There are some vertebrate fossils of late-middle Eocene age, suggesting intermittent land, but evidence for an extensive and sustained terrestrial biota is meager. This means that the island was submerged for most of this interval (~42–10 Ma) and that the modern biota is geologically of recent origin (Buskirk, 1985) resulting from introductions by dispersal since near the end of the Miocene. There is no definitive evidence that Jamaica was ever directly connected to any other landmass during the Late Cretaceous and certainly not since the late Miocene, which precludes vicariance as the principal means of distribution and as an evolutionary mechanism in the origin of the present biota.

Hispaniola—

> "Driver of Phoebus' chariot, Phaëton, Struck by Jove's thunder, rests beneath this stone, He could not rule his father's car of fire, Yet was it much so noble to aspire. His sisters, the Heliades, as they lamented his fate were turned into poplar trees on the banks of the river, and their tears, which continued to flow, became amber as they dropped into the stream." (From Thomas Bulfinch, 1998, *The Illustrated Age of Fable*, Stewart, Tabori & Chang, New York)

Although the late-early through early-middle Miocene Dominican amber (20–15 Ma; Iturralde-Vinent & MacPhee, 1996) has been the center of much recent economic, paleontologic (Poinar & Poinar, 1999), and cinematic interest, other mineral resources were pivotal in the early settlement of the New World by the Spaniards and in furthering later studies on the geology of Hispaniola. On his first voyage, Columbus and his crew were alerted to the presence of gold by the orna-

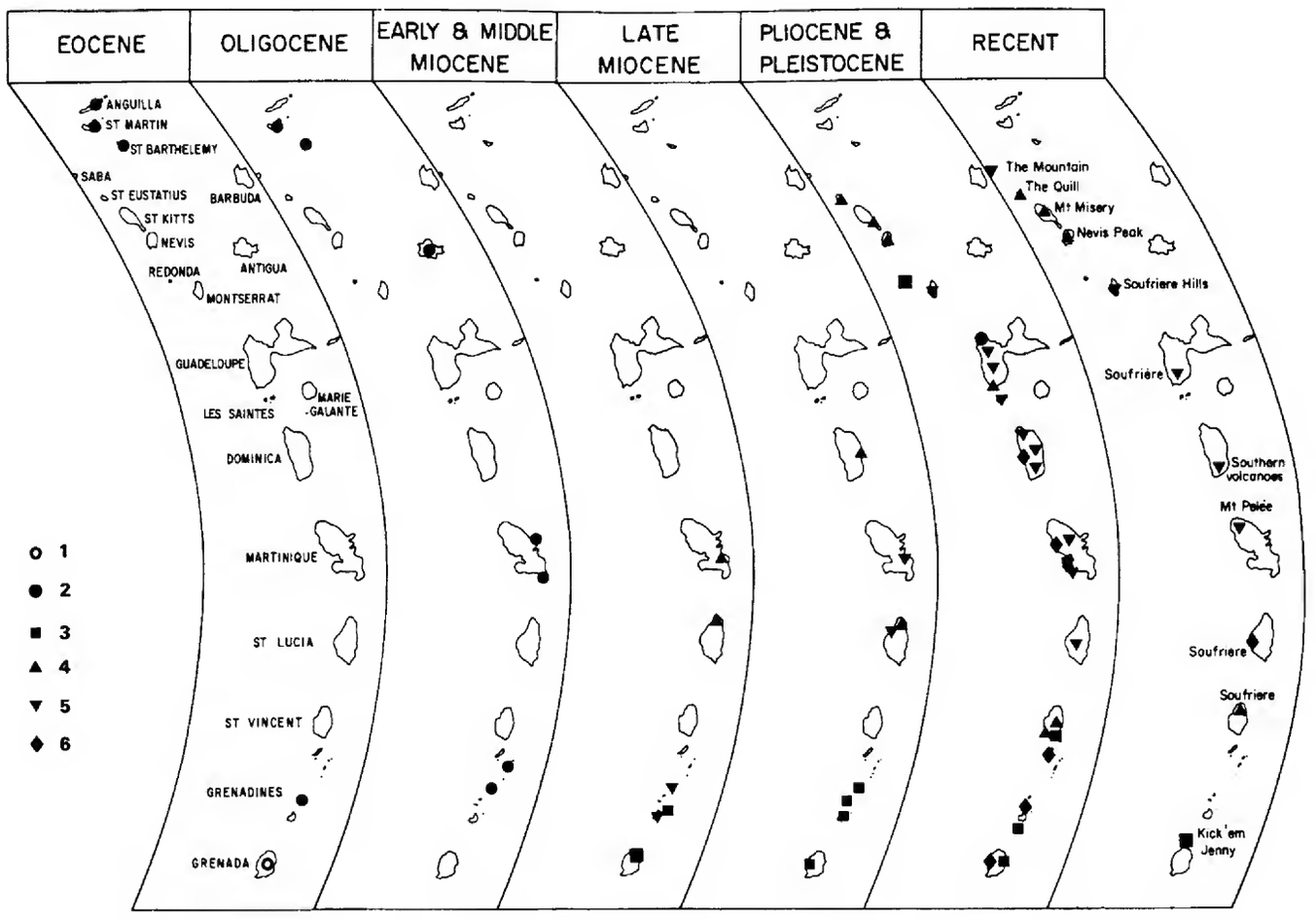


Figure 2.23. Location of main Cenozoic volcanic series in the Lesser Antilles. Symbol 1, volcanism of unknown affinity; 2, orogenic-type volcanism (precise affinities unknown); 3, Mg-rich alkalic or subalkalic basalts and associated rocks; 4, low-K volcanic series; 5, medium-K volcanic series; 6, high-K volcanic series. From Maury et al. (1990), courtesy of the Geological Society of America.

ments worn by the native population. In January 1493, they stopped to fill water barrels where the Río Yaque del Norte of Hispaniola empties into the Caribbean Sea, and small pieces of gold were found lodged in the metal hoops of the barrels. The river drains the Cibao Valley of northern Hispaniola, and the discovery eventually led to the establishment of numerous gold mines in the Caribbean region. Five hundred years later, alluvial gold is still panned from streams flowing from the southern flanks of the Cibao Valley, and the largest gold mine in the Western Hemisphere, Pueblo Viejo in central Hispaniola (Russell & Kesler, 1991), is at the site of early Spanish diggings. The first study of Caribbean geology, on the French colony of Saint Domingue, now Haiti, was by the Frenchman Dupuget (1796; Draper & Dengo, 1990).

The Cordillera Central–Massif du Nord of Hispaniola (Fig. 1.16) formed in the latest Cretaceous and its principal uplift occurred between 3 and 4 Ma and continues into modern time. As noted earlier, a land fragment consisting of present-day eastern Cuba, northwestern Hispaniola, and Puerto Rico was sutured on to eastern Cuba in the middle Eocene, while continued movement of the Caribbean Plate fully separated Puerto Rico from Hispaniola in the Oligocene–early Miocene and western Hispaniola from Cuba by the early to middle Miocene (20–25 Ma). Southern Hispaniola was added on to the main island in about the middle Miocene (~15 Ma). The contact is represented by the modern Cul-de-Sac/Enriquillo Basin region (Fig. 1.11; Maurrasse, 1982). The downward folding of the Cibao Basin occurred in the early Miocene (Gordon et al., 1997, p. 10,078), and it was subsequently uplifted to convert the 225-km-long seaway into a valley now filled with alluvial sediment. The southern peninsula was fully emergent by the Plio–Pleistocene, and the eastern peninsula (Llanos Costeros del Seibo, a raised coral reef) appeared in the Pleistocene. A geologic map of Hispaniola is available on the geologic information page of the Caribbean Geology and Tectonics Web site (http://www.fiu.edu/orgs/caribgeol/).

A comparison of the geographic (Fig. 1.16) and geologic (Fig. 2.22) maps of the Dominican Republic shows that highlands, likely bordered by coastal swamps and mangroves with intervening valleys and seaways, prevailed throughout the late Cenozoic. Within the Cibao Valley, there is the smaller Bonao Valley that in the Quaternary was a lake ~8 × 20 km that subsequently has been filled with alluvial sediments. Similarly, the Valley of San Juan de la Maguana is situated between the Cordillera Central and Sierra de Neiba (Fig. 1.16). Prior to the Miocene, this was a lake with drainage via the Yaque del Sur and Artibonite rivers (Bolay, 1997). It has been elevated and filled with lacustrine sediments. Such sites provide ideal, albeit local and restricted, localities for the preservation of plant fossils. Some plant-bearing sites are known (e.g., the Mio–Pliocene megafossil and microfossil Artibonite flora of Haiti; the megafossil Samaná [Sánchez] Province flora of northern Dominican Republic), but the megafossil floras were studied in the early 1900s and have not been revised, and there are no current efforts to locate new ones. Field studies in these often remote regions, covered by dense vegetation, are difficult, but sustained exploration by resident scientists would undoubtedly reveal new floras in both Haiti and the Dominican Republic that would be of considerable interest and importance.

Puerto Rico—Proto-Puerto Rico was part of the isthmian volcanic island arc of the Late Jurassic and Early Cretaceous. The central igneous province was uplifted near the K/T boundary, and most of the island was probably emergent by the middle Eocene. Puerto Rico arrived at or near its present position during the late Eocene to early Oligocene (37–33 Ma), and it separated from Hispaniola later in the Oligocene–early

Miocene. The central igneous province is bordered on the north and south by middle Oligocene to late Miocene–Pliocene carbonate and clastic deposits (Lewis & Draper, 1990). The oldest rocks of the northern carbonate province belong to the middle Oligocene San Sebastián Formation, which contains a rich plant mega- and microfossil assemblage. The early Oligocene Juana Díaz Formation near Yauco in southwestern Puerto Rico is the oldest in the southern carbonate province and contains an important mammalian fauna. Lewis and Draper (1990, p. 120) believe that subsidence took place between the middle Eocene and middle Oligocene, then between the middle Oligocene and Pliocene: "Most of Puerto Rico was probably submerged during the whole of this time." However, lignites and the extensive land flora preserved in the middle Oligocene San Sebastián Formation reveal the presence of densely vegetated uplands at this time.

Virgin Islands—The Virgin Islands terminate the Greater Antilles chain to the east. The oldest rocks belong to the Water Island Formation of Cretaceous (Albian) age, but, consistent with the history of other islands of the Greater Antilles, the principal period of uplift was in the late Eocene.

In some of the older geologic (mostly vertebrate paleontological) and biogeographic literature, Cuba and other islands of the Greater Antilles are shown far south of their present position. For example, Corrall (1939) places the islands along the north coast of South America as recently as the late Miocene (Borhidi, 1996, p. 257), and Vandel (1973) used this reconstruction to explain similarities in vertebrate faunas between Cuba and South America. There is no geologic evidence that the Antilles bordered northern South America anytime during the Late Cretaceous or Cenozoic.

This does not necessarily mean, however, that land continuity was not greater in the past. Iturralde-Vinent and MacPhee (1999) believe, on the basis of their interpretation of the geological and terrestrial vertebrate faunal evidence, that at the Eocene–Oligocene transition there was a period of uplift (part of the global Pyrenean uplift) and a simultaneous fall in sea level. Stratigraphic sections have a minimum of marine sediments, and terrestrial sediments were widespread at this time. As a result, they believe that during a 3-Ma-year interval between 32 and 29 Ma, there was a greater extent of subaerial exposure than perhaps in all of the Cenozoic including modern times, and that a continuous or near-continuous connection of islands and peninsulas existed between northern South America and Puerto Rico via the Aves Ridge (GAARlandia = Greater Antilles plus Aves Ridge). Undoubtedly, vigorous assessment of this model will be forthcoming from geologists and taxonomic specialists in the various plant and animal groups (e.g., Graham, 2003; Hedges, 2006).

The Lesser Antilles—These islands continued to move relatively eastward after the Greater Antilles collided with the Bahamas Platform in the Eocene. They are located over the subduction zone where the Atlantic Ocean crust dips beneath the Caribbean Plate. Subduction still continues, at the comparatively slow rate of about 2–4 cm/yr (MacDonald et al., 2000),

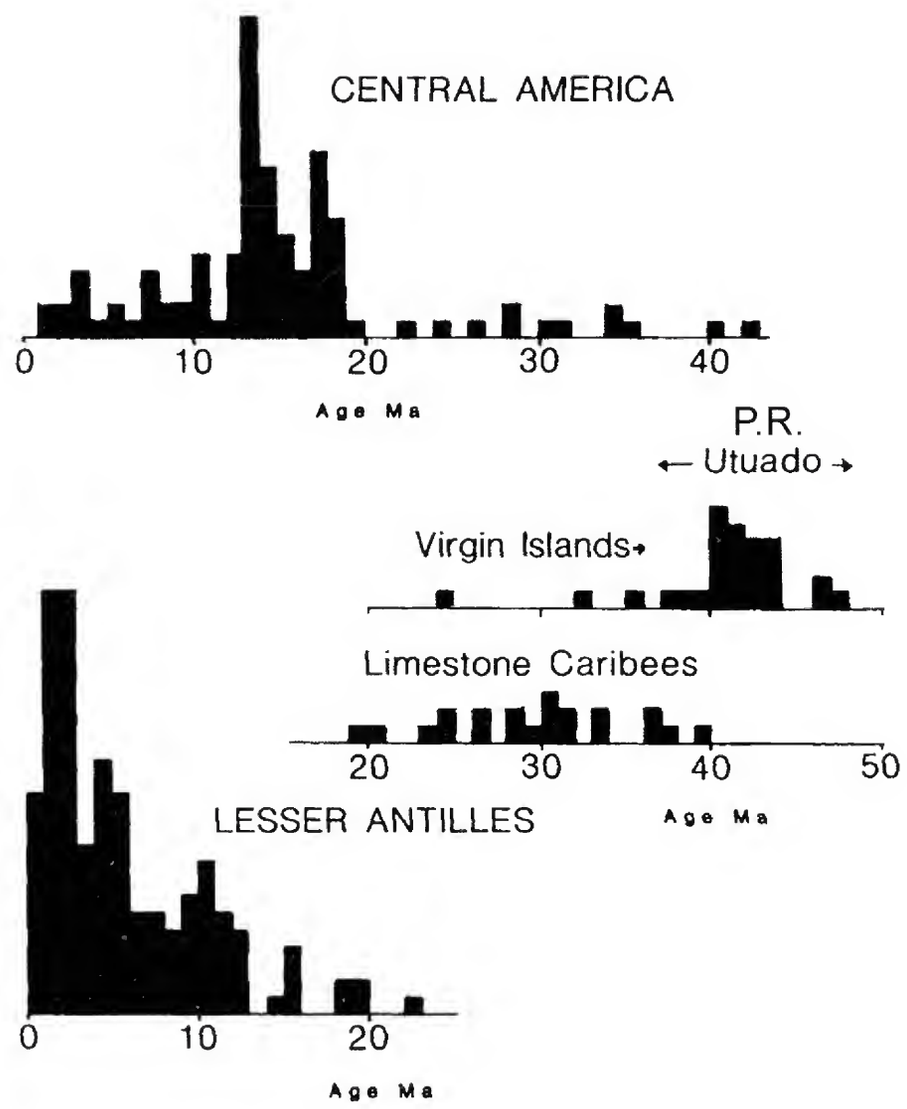


Figure 2.24. K/Ar ages for Tertiary volcanism in the Antilles. Note the later age of volcanic activity/island formation from the west (Virgin Islands) to the east and south (Limestone Caribees, Lesser Antilles). From Donnelly et al. (1990b), courtesy of the Geological Society of America.

with accompanying volcanism, and the islands are among the few active arcs in the Atlantic Ocean (Maury et al., 1990). The principal period of emergence was somewhat later than for the Greater Antilles, but much of the early history is buried beneath volcanics.

Extending from northeastern South America, the Lesser Antilles consist of a single line of islands—Grenada, the Grenadines, St. Vincent, St. Lucia, and Martinique[1] (Fig. 2.23). The rocks here were mostly uplifted in the middle Eocene to early Miocene (Mayreau Basalt; Speed et al., 1993), and magmas of Neogene age erupted at the surface ~12 Ma. Although Barbados is geographically included in the Lesser Antilles, it is structurally separated from them by the Tobago Trough. The island is the highest and only emergent peak of the Barbados Ridge that developed ~50 Ma, with Barbados appearing as an island only in the Pleistocene (~1 Ma; Speed & Keller, 1993). The dates indicate there was less land available for migration through the Lesser Antilles in the past than at present (Fig. 2.24).

North of Martinique, the Lesser Antilles divide into a double arc system consisting of an older northeastern outer arc (Antigua, Barbuda, St. Bartholomew, and others; the Limestone Caribees or Leeward Islands; middle Eocene to Oligocene) and a northwestern inner arc of young volcanic islands (Dominica, Montserrat, St. Kitts, and others; the Windward

Islands; late Miocene and younger; Figs. 2.23, 2.24; Chapter 1, Note 7). Some islands of the outer arc were probably emergent by the middle to late Eocene, and a fragmented migrational pathway between South America and North America through this sector probably dates from this period.

Summary

It is well established that the early history of the Gulf of Mexico–Caribbean Basin began in the Jurassic with the separation of South America (and Africa) from North America and the opening of the southern Atlantic Ocean. Following the model of Pindell and Barrett (1990; Pindell, 1994) and others (e.g., Iturralde-Vinent, 1978, 1994), the subsequent events may be summarized as follows:

1. Origin of the proto-Greater Antilles as a submerged volcanic island arc in the present-day isthmian region in the Early Cretaceous (Valanginian, ~130 Ma).
2. Collision of the mostly submerged volcanic island arc with the Bahamas Platform in the late Paleocene and earliest Eocene (~56 Ma).
3. Early and sustained emergence of most of the proto-Greater Antilles in the middle Eocene (~49 Ma).
4. Eastern Cuba (plus northern Hispaniola and Puerto Rico) added to western-central Cuba in the early to middle Eocene.
5. Western and central Cuba structurally connected by the late middle Eocene, but land surfaces disrupted by the Havana–Matanzas Channel.
6. Dry land across the various parts of Cuba established in the late Miocene.
7. Western and northern Hispaniola and Puerto Rico separated from eastern Cuba in the early to middle Miocene.
8. Southern Hispaniola added on to northern Hispaniola in the middle Miocene.
9. Puerto Rico separated from Hispaniola in the Oligocene–early Miocene.
10. Jamaica re-emerged in the late Miocene.
11. The Virgin Islands emerged in the late Eocene.
12. The Lesser Antilles emerged between the middle Eocene (in the north) and the Oligocene (in the south).

Among the climatic implications of this geologic scenario are that because of their geographic location and insular history the Antilles have been comparatively insulated by warm Caribbean currents from incursions of cold northern fronts (Watts & Hansen, 1994). For much of their history, they have been under the descending arm of the Hadley regime with a pressure system called the Bermuda–Azores High. During extreme climatic changes, such as at the glacial maxima to the north, temperature–precipitation fluctuations did occur. Schubert and Medina (1982) interpreted geomorphic structures evident on aerial photographs of the highest peaks of the Dominican Republic to be of glacial origin, and subsequent field studies of these "modest cirques and inferred moraine deposits" (Orvis et al., 1997, 2002) suggest this may possibly be true. Strontium in Barbados corals indicate the surrounding waters cooled by ~5° C at the glacial maxima (Guilderson et al., 1994).

After the Antilles were in position, and while details of their physiography were being refined, a second volcanic island arc began to form in the isthmian region that would later provide continuous land between the continents.

CENTRAL AMERICA

Studies on the geology of Central America began mostly in the middle 1800s by those seeking gold locally and by others crossing the region to seek gold in California. For example, William Wells (1857) discovered gold in Honduras and described the geology adjacent to the mine. Later Seebach (1892) published an account of the volcanic chain that runs through much of Central America (Fig. 2.25); Dollfus and Montserrat (1868) published the first geological map of Guatemala and El Salvador; and Gabb (1874a, b, 1875) studied the geology of the Cordillera de Talamanca of Costa Rica.

Subsequent investigations revealed that the geology of northern Central America (Guatemala, Belize, Honduras, El Salvador, northern Nicaragua) differed from that of southern Central America (southern Nicaragua, Costa Rica, Panama; Vaughan, 1918; Woodring, 1928; Schuchert, 1935). Schuchert (1935) first applied the terms "Nuclear Central America" and "Isthmian Link" to these two regions, respectively, and Dengo (1969a, b) later divided Nuclear Central America into the Maya (Yucatán) and Chortis blocks (Escalante, 1990; Fig. 2.26). Other important early studies were made by Dengo and Bohnenberger (1969) and Weyl (1961, 1980).

The northern boundary of the Maya Block is a crustal suture known as Salina Cruz across the Isthmus of Tehuantepec. The contact between the Maya and Chortis blocks is the Polochic–Motagua Fault Zone in northern Guatemala, and the southern limit of the Chortis Block is along the Santa Elena (onshore)–Hess Escarpment (eastern offshore) zone just south of Lago Nicaragua (Fig. 2.27). The western terminus of the Santa Elena suture is at the Middle American Trench. The two blocks represent exotic terranes, and although their exact origin is uncertain, the Maya Block was situated in the present Gulf of Mexico region in the Jurassic and moved slightly southwestward as South America separated from North America. The Chortis Block came from a greater distance along the west coast of Mexico and moved southeastward during the Mesozoic. Although the position of the Chortis Block has been placed out in the Pacific Ocean by some authors, Donnelly (1985, p. 115; 1989a) notes that the presence of Early

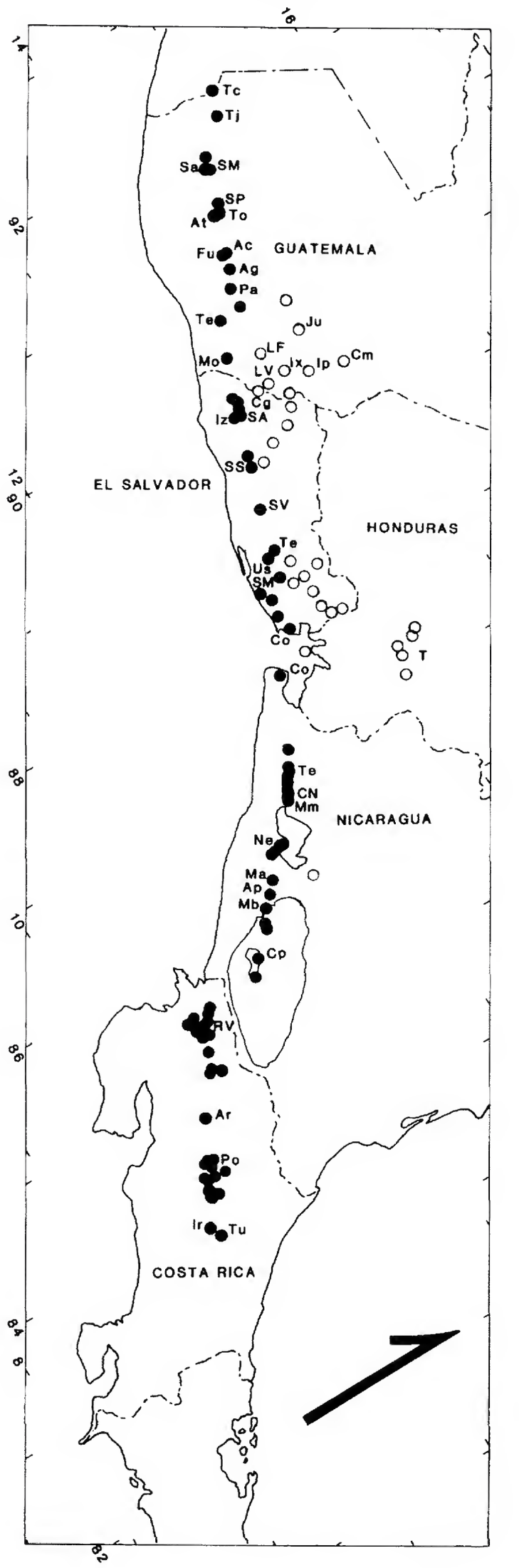


Figure 2.25. Active volcanic centers of Central America. Guatemala: Tc, Tacaná; Tj, Tajumulco; SM, Santa María; Sa, Santiaguito; SP, San Pedro; To, Tolimán; At, Atitlán; Ac, Acatenango; Fu, Fuego; Ag, Agua; Pa, Pacaya; Te, Tecuamburro; Mo, Moyuta; Ju, Jumay; Cm, Chiquimula; Ip, Ipala; Ix, Ixtepeque; LF, Las Flores; LV, Cerro Las Víboras. El Salvador: Cg, Chingo; Iz, Izalco; SA, Santa Ana; SS, San Salvador; Te, Tecapa; Us, Usulután; SM, San Miguel; Co, Conchagua. Honduras: T, Tegucigalpa. Nicaragua: Co, Cosegüina; Te, Telica; CN, Cerro Negro; Mm, Momotombo; Ne, Nejapa alignment; Ma, Masaya; Ap, Apoyo; Mb, Mombacho; Cp, Concepción. Costa Rica: RV, Rincón de las Viejas; Ar, Arenal; Po, Poas; Ir, Irazú; Tu, Turrialba. From Donnelly et al. (1990b), courtesy of Geological Society of America.

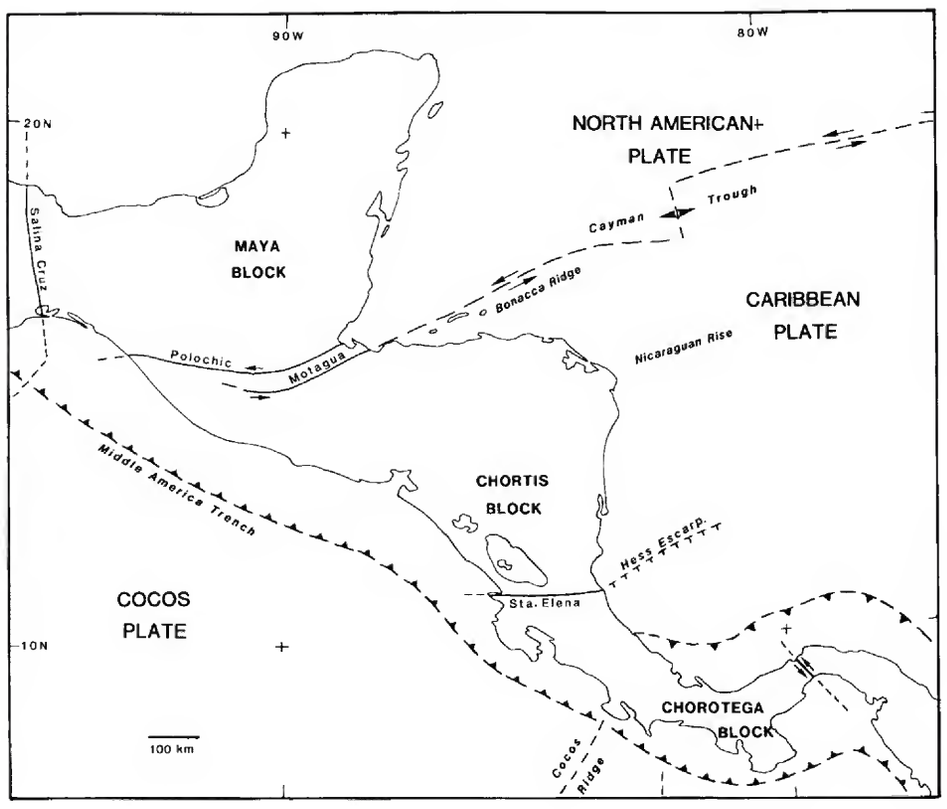


Figure 2.26. Regional tectonic features of northern Central America. From Donnelly et al. (1990a), courtesy of Geological Society of America.

Cretaceous red beds requires it be within the rain shadow of a continental landmass to produce the arid conditions necessary for deep red bed development (viz., oxidation to great depths; but see Sheldon, 2005). The two blocks were sutured together by the latest Cretaceous as indicated by Ar 39/40 radiometric dates ranging between 66 and 70 Ma on ophiolites at the contact (Donnelly, 1989a; Donnelly et al., 1990a). Ophiolites are deep-sea sediments associated with basalts representing original oceanic crust or back-arc basin extrusions and mark the contact between colliding terranes. The Cordillera de los Cuchumatanes within the Maya Block was formed during the Cretaceous, uplifted in the Pliocene from subduction along the Middle American Trench (Dengo & Bohnenberger, 1969; Weyl, 1980), and glaciated in the Quaternary as evident by U-shaped valleys at sites ~3600 m in elevation (Anderson, 1968; Hastenrath, 1973).

Southern Central America (Costa Rica, Panama) is especially complex because it is located at the contact between the Caribbean, Cocos, Nazca, and South American plates (Fig. 2.27). The Cocos and Nazca plates resulted from the fragmentation of the older Farallon Plate at the end of the Eocene. The Cocos and Caribbean plates are converging at the rate of ~8 cm/yr along the Middle American Trench, and volcanoes developed at the surface above the Benioff Zone. The Nicoya Peninsula of Costa Rica contains basaltic basement rocks of Jurassic to Late Cretaceous (Donnelly, 1994; Sinton et al., 1997) to possibly Eocene age (Drummond et al., 1995), which began uplift by the Late Cretaceous (Castillo-Muñoz, 1983, 1984; Dengo, 1969a; Donnelly, 1994, p. 35). It is an exotic (transported) or suspect terrane (full history not known), and like the Osa, Burica, and Azuero peninsulas (see Fig. 2.30), it represents one of the land fragments moving relatively eastward during the Paleogene. The Cordillera de Talamanca resulted from subduction of the Cocos Ridge beneath the volcanic arc, and collision of the arc with the South American Plate. It reached near-present elevation in the Pliocene (~3 Ma) and was glaciated in the Quaternary (Hastenrath, 1973; Horn & Haberyan, 1993).

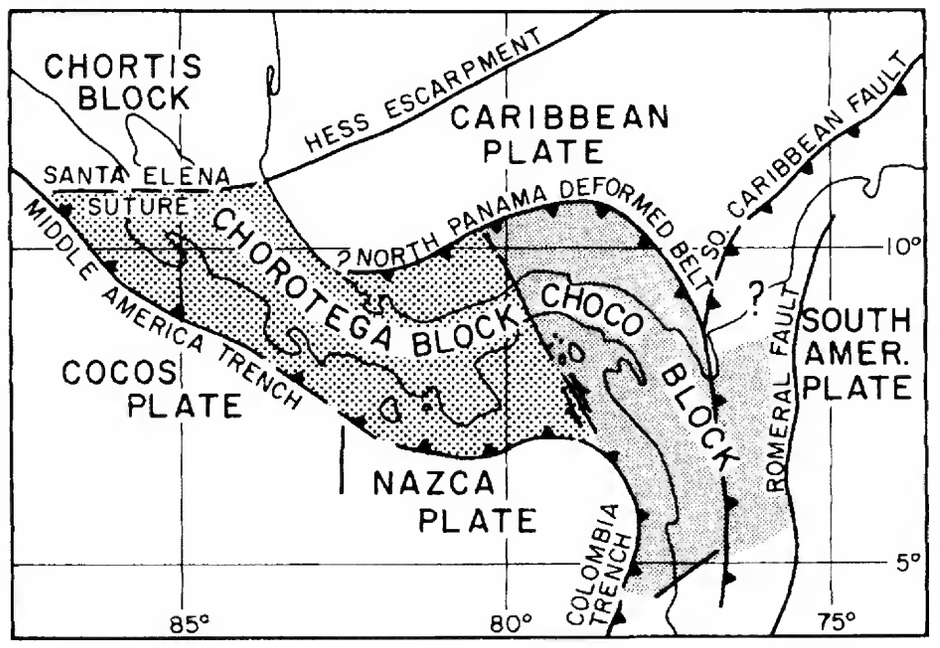


Figure 2.27. Regional tectonic features of southern Central America. From Escalante (1990), courtesy of the Geological Society of America.

A complex of sediments of paleobotanical interest is the Limón Group (formerly the Uscari Sequence) exposed ~45 km inland from the Caribbean Sea in Costa Rica near the Panama border. Correlation of Neogene deposits in southern Central America has improved considerably through the Panama Paleontology Project (Collins & Coates, 1999). In the older charts of Cooke et al. (1943) and Castillo-Muñoz (1983), the Uscari Shale is placed in the upper Oligocene to lower Miocene. It is overlain unconformably by sandstone containing both plant mega- and microfossils. The sandstone is in the Río Banano Formation, earlier regarded as Miocene and likely

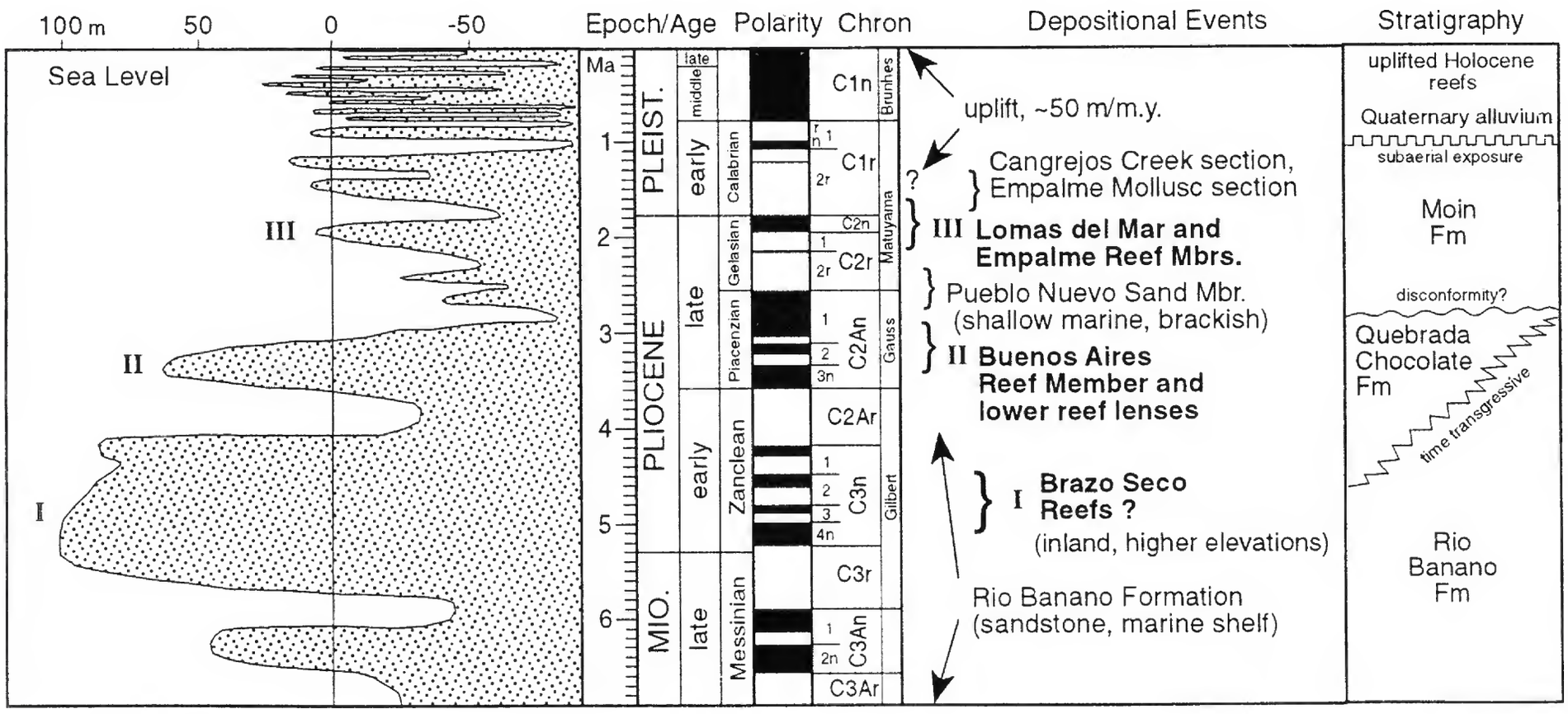


Figure 2.28. Río Banano Formation and global sea-level events, Limón Group, Costa Rica. From McNeill et al. (2000), courtesy of the Geological Society of America.

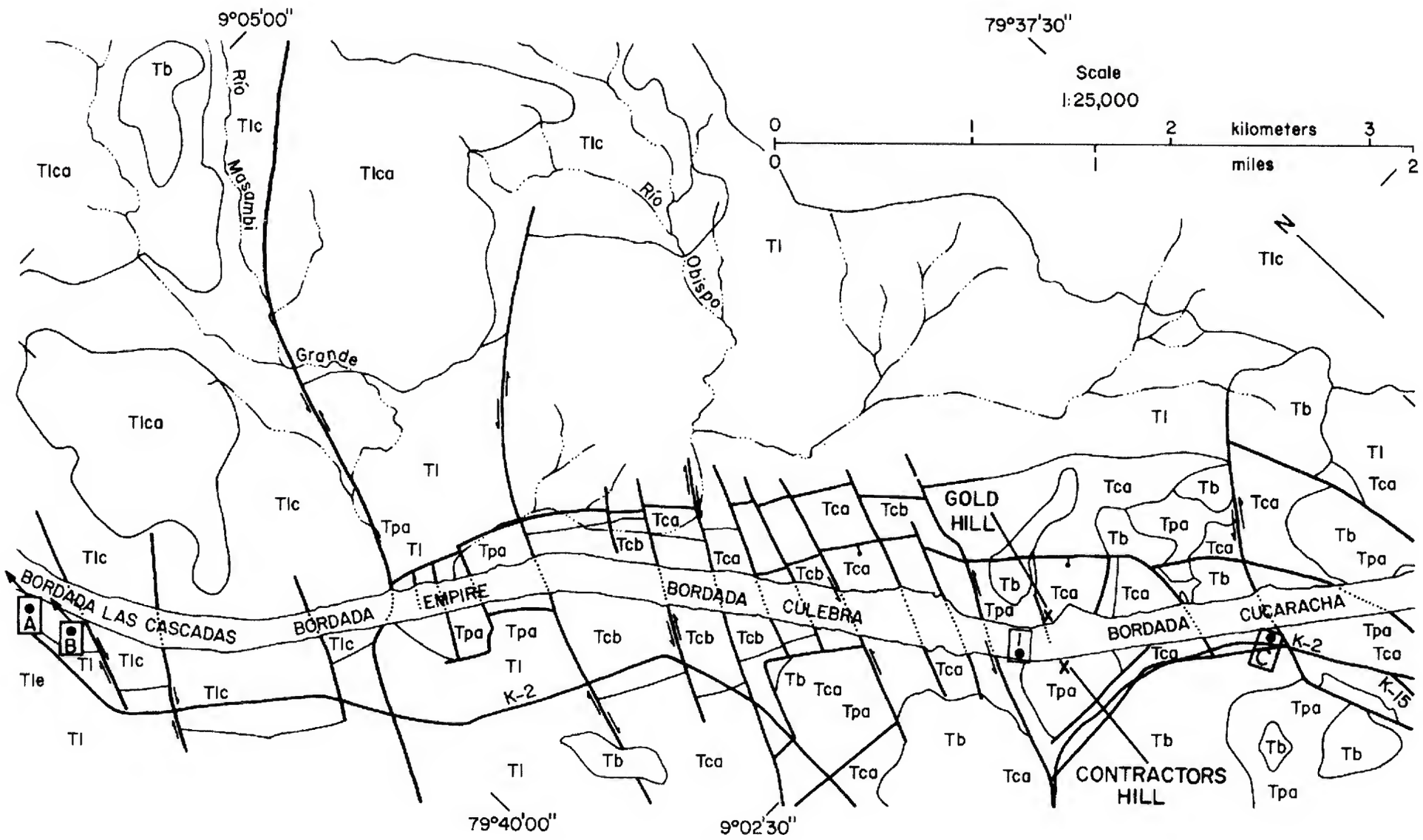


Figure 2.29. Generalized surface geology map, Gaillard Cut section, Panama Canal. Note extensive faulting. A, B indicate plant microfossil-collecting localities in the La Boca Formation; C in the Cucaracha Formation (Chapter 4). Tlc, Las Cascadas Formation; Tl, La Boca; Tle, Emperador Limestone Member (coralliferous limestone) of La Boca Formation; Tpa, Pedro Miguel; Tcb, Culebra; Tca, Cucaracha; Tca, andesite, equal in age to Las Cascadas Formation (early Miocene); Tb, intrusive and extrusive basalts (middle and late Miocene). Modified from Stewart and Stewart (1980), courtesy of U.S. Geological Survey.

late Miocene, but now considered Pliocene in age (Collins & Coates, 1999; McNeill et al., 2000; Fig. 2.28). Plant microfossils are known from the Río Banano Formation at another locality about 30 km west-southwest of Limón. These sediments were earlier placed in the Plio–Pleistocene (Taylor, 1975; Escalante, 1990), but they have been radiometrically dated at 3.6–2.5 Ma and are closer to late Pliocene in age (Coates et al., 1992; Collins & Coates, 1999; Chapter 6). The formations of the Limón Group are of interest because they record the emergence of the isthmus in the region. They show a sequence from bathyal to middle-shelf depths (~500–300 m) in the lower and middle parts of the Uscari Formation, to near-shore marine and delta deposits (<20 m) in the overlying Pliocene Río Banano Formation (McNeill et al., 2000, and references cited therein).

These coastal sediments record late Pliocene and early Pleistocene eustatic changes in sea level. There was an early Pliocene highstand, also evident in deposits from the Bahamas. There followed a second highstand at the early–late Pliocene boundary into the early–late Pliocene (~3.5–3 Ma), evident on the global sea level curve (Haq et al., 1987) and also noted by Dowsett and Cronin (1990) on the Atlantic Coastal Plain of the southeastern United States. This was about the time the Paraje Solo flora of Veracruz, Mexico, the Herrería flora of Guatemala, and the Río Banano flora of Costa Rica were being deposited. Reef corals began to form, reflecting the rising sea level as well as warm-temperate to tropical conditions. At ~3.2–2.4 Ma there was a drop in sea level marking the expansion of glaciation in the Northern Hemisphere.

Faulting has been widespread throughout southern Central America during Late Cretaceous and Cenozoic time and this has resulted in numerous outcrops and subsurface units of limited extent and complicated stratigraphic relationships. Along the Las Cascadas Reach section of the Panama Canal, 113 faults are evident in a distance of only 3 km (Fig. 2.29). Fortunately, the economic and strategic importance of the Panama Canal requires a detailed knowledge of the geology and geologic processes affecting its maintenance and operation. In this regard, a localized feature of the region is the inverted topography. During the Cenozoic, streams of lava flowed through valleys and formed hard layers surrounded by softer sediments in the uplands. Erosion of the softer sediments eventually placed the once low-elevation valley lava in the position of cap rock. When the Panama Canal was cut through this setting, the heavy overlying lava began forcing the softer sediments into the canal, requiring expensive and perpetual dredging.

The various maps, surveys, logs, and cores from drilling operations by the Panama Canal Company have provided invaluable resources for studies of the geology and paleontology

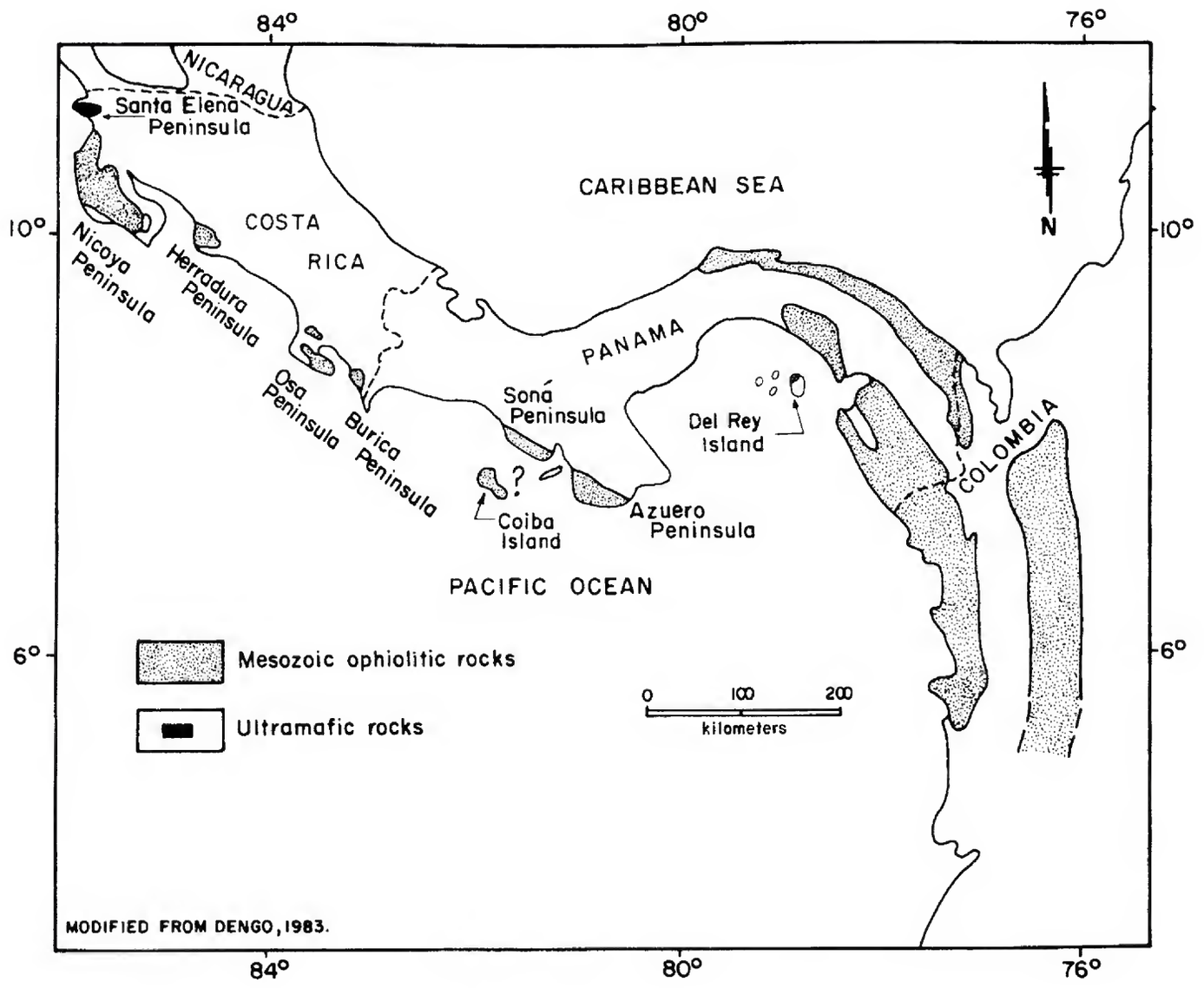


Figure 2.30. Distribution of basement rocks in southern Central America and western Colombia. From Escalante (1990), courtesy of the Geological Society of America.

of the former Canal Zone and adjacent regions. Similarly, the Smithsonian Tropical Research Institute in Balboa, and its field station on Barro Colorado Island in Gatún Lake, are centers for a broad array of investigations. The ~12-mile-wide former Canal Zone across central Panama is as well known geologically and biologically as any comparable area in tropical America, and it contains extensive floras and faunas of Cenozoic age.

Two aspects of southern Central American geology particularly relevant to biogeography are the paleophysiography of the region during the Late Cretaceous and Cenozoic, and the timing of the uplift of the Panama land bridge. The scenario can be a bit circular because some of the evidence used to estimate the time of uplift, and thus explain the migratory history of the biota across the isthmus (and marine migrations barred by it), is the migratory history itself; that is, the patterns of similarity and differences in Cenozoic fossil faunas and floras on either side of the isthmus. Independent geological and geochemical evidence exists, however, and reconstructions based on structural geology, tectonic history, sediment analysis, and paleontological information are proving mutually consistent.

A visualization of this history can be gained by examining a map of the basement rocks of southern Central America (Fig. 2.30). The region consisted of islands and peninsulas of low to moderate relief during the early and middle Cenozoic, while in the late Cenozoic, volcanism and uplift from subduction and compression episodically elevated the intervening lands into a continuous connection. The accreted Azuero, Burica, Nicoya, Osa, and Santa Elena peninsulas of Costa Rica and Panama are examples, and they formed by subduction of the Cocos and Coiba ridges into the Middle American Trench. The biogeographic expectations of this history are that early migrations across the isthmus would be by organisms primarily of lowland tropical habitats capable of dispersal across marine barriers, and through chance long-distance dispersal by hurricanes, migratory birds, and flotsam-jetsam. Later, conditions would become increasingly favorable for the migration of organisms of upland, more temperate habitats and those with less effective means of long-distance dispersal. The terrestrial plant fossil record shows a low level of similarity between the biota of southern Central America and adjacent northern South America during the Early and Middle Tertiary, while progressively greater similarities developed in the Late Tertiary and Quaternary (Chapter 8). Woodring (1966) has pointed out that a land bridge constitutes a sea barrier and, indeed, the distinction between marine biotas of the western equatorial Atlantic Ocean, the Caribbean Sea, and the eastern Pacific Ocean follows a pattern reciprocal to that of the terrestrial flora and fauna. As expected, this differentiation begins with benthic (ocean-bottom) organisms, and becomes evident only later among planktic (surface-water) organisms.

One line of geological evidence useful for establishing the timing of uplift, independent of the paleontological data, is chemical analysis of pelagic (open-ocean) sediments (Donnelly, 1989b). Surface waters of the Atlantic and Pacific oceans

are relatively silica free because the silica is removed by planktic organisms for constructing their skeletal material. Upon death, the walls drift down through intermediate-depth water and accumulate on the ocean floor; the silica is brought back to the surface by upwelling, especially strong in the northern and southern Atlantic Ocean, where it is again removed by the metabolism of surface organisms. Thus, surface ocean waters are relatively low in silica, while intermediate-depth and bottom waters have a higher silica content. The water that passes from the Pacific to the Atlantic through the southern ocean is mostly surface water that is low in silica content, while that flowing from the Atlantic to the Pacific is mostly intermediate-depth water that is comparatively rich in silica. The result is that bottom and intermediate-depth waters of the Pacific have a distinctively higher silica signature than those of the Atlantic.

Analysis of DSDP cores reveals a three-part history of silica concentration in Pacific, Atlantic, and Caribbean waters. First, in the Late Cretaceous and early Cenozoic, all waters have a similar silica content indicating open circulation between the three ocean basins. Differences become evident between the Atlantic and the Pacific oceans in the late Eocene (formation of the emergent proto-Antilles), and finally between the Atlantic and Pacific oceans and the Caribbean Sea beginning in the latest Oligocene to middle Miocene (~15 Ma, beginning of the formation of the isthmian connection and isolation of the Caribbean Sea). The biogeographic implications of results from chemical analysis of the ocean sediments have been noted by Donnelly (1989b, p. 107): "We can set at rest…any ideas of a [Late Cretaceous to] Paleocene island arc connection between the Americas such that might explain similarities, for example, between edentate, notoungulate, and dinothere faunas of North and South America (Gingerich, 1985). Either these early mammals dispersed across a substantial width of ocean or dispersed by some more complicated pathway… ."

The chemical distinction of the Caribbean surface water becomes evident at ~4.1 Ma (Keigwin, 1982; Donnelly, 1989a), indicating almost complete connection across the isthmus. The final link to be forged was through the present Darién Province of Panama and the adjacent Atrato region of northwestern Colombia. This was accomplished near the early–late Pliocene boundary between ~3.7 and 3.2 Ma (Fig. 2.31) and allowed the direct overland migration of organisms of lowland tropical habitats. After initial completion, the bridge may have been breached briefly due to higher sea levels at the end of the middle Pliocene warm interval (MPWI; 3.2–2.8 Ma) and during some of the interglacials. By about 2.5 Ma local uplands of sufficient elevation had developed to initiate the increasing

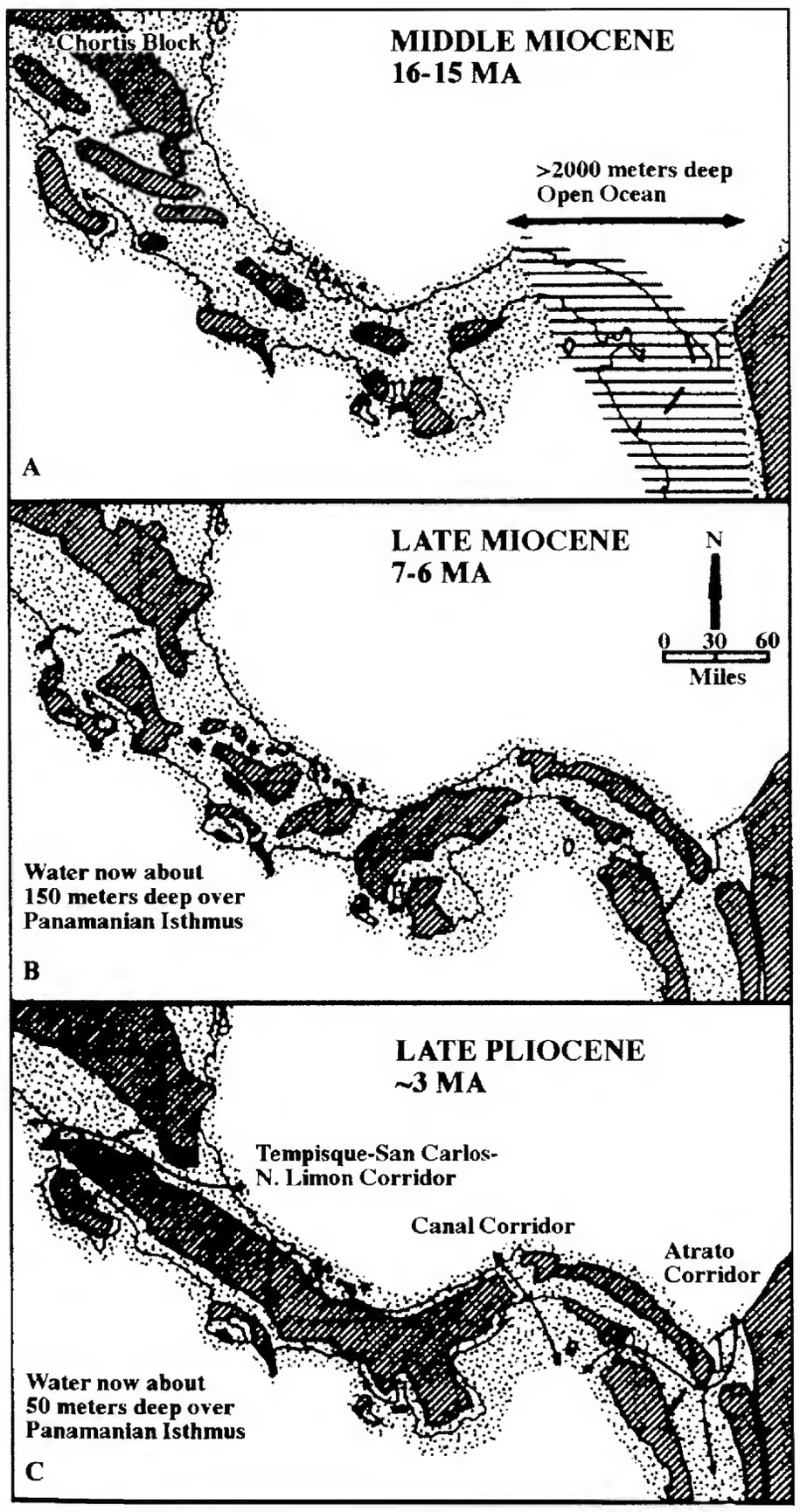


Figure 2.31. Paleogeographic interpretation of the Central American isthmus in (A) the middle Miocene, 15 Ma; (B) the late Miocene, 6 Ma; and (C) at the end of the Pliocene, 3 Ma. From Coates (1997, p. 23). Used with permission of Yale University Press, New Haven, Connecticut.

distinction between a generally wetter Atlantic side and a drier Pacific side, and to permit the migration of more highland and temperate elements. Northern temperate genera with moderate or little means of long-distance dispersal, such as *Alnus*, first appear in northern South America ~1 Ma, and *Quercus* at ~330 Kyr (Hooghiemstra & Ran, 1994).

SOUTH AMERICA

"Thomas Burnet, an English theologian of the seventeenth century, is remembered today only because he wrote one of the funniest books in the history of Protestant pseudoscience: *Telluris Theoria Sacra* (Sacred Theory of the Earth), London, 1681. Before the Flood, Burnet argues, the earth was hollow, filled with water, and perfectly smooth like an egg. There were no seas, no valleys, and no mountains. The climate was perpetually spring-like, the sunny weather broken only by occasional gentle rains. But men were long-lived, like Methuselah, which gave them plenty of leisure time for wickedness. God destroyed the corrupt earth by crushing it until the shell cracked, letting out the waters of the deluge. Once egg-perfect, the earth now became a 'rude lump…a little dirty planet.' The crumpled shell formed mountains [and basins] and the flood waters collected in low areas to make the oceans." (From M. Gardner, 1965, *The Annotated Ancient Mariner*, Potter, Inc., New York. p. 36)

The first geological survey of South America was made by Alexander von Humboldt between 1799 and 1804 during his travels with Aimée Bonpland through Venezuela, Colombia, and Ecuador (Humboldt, 1852; Chazdon & the Earl of Cranbrook, 2002). In addition to gold mentioned previously and copper, tin, and zinc discovered later, oil has long been a powerful catalyst for the study of South American geology. The first discovery of oil in the New World, by Europeans, was by the Spaniard Juan de Castellanos in 1589 from a seepage on the island of Cubagua off the coast of Venezuela. Humboldt (1814–1829; see ref. 1852) in his *Narrative of Travels* records that "in crossing the arid hills of Cape Cirial [Venezuela], we noticed a strong smell of petroleum, which the first historian of this country, Oviedo, called 'a resinous aromatic and medicinal liquor.' Near Cape de La Brea, the petroleum covers the surface of the sea more than a thousand feet from the coast." Today, the Tertiary of the oil-rich Maracaibo Basin has been studied in greater detail than any other geologic section in the world. General sources of information on the geology of South America include the Commission de la Carte Géologique du Monde's (1964) Carte Géologique de L'Amérique du Sud and the digitized Geologic Map of South

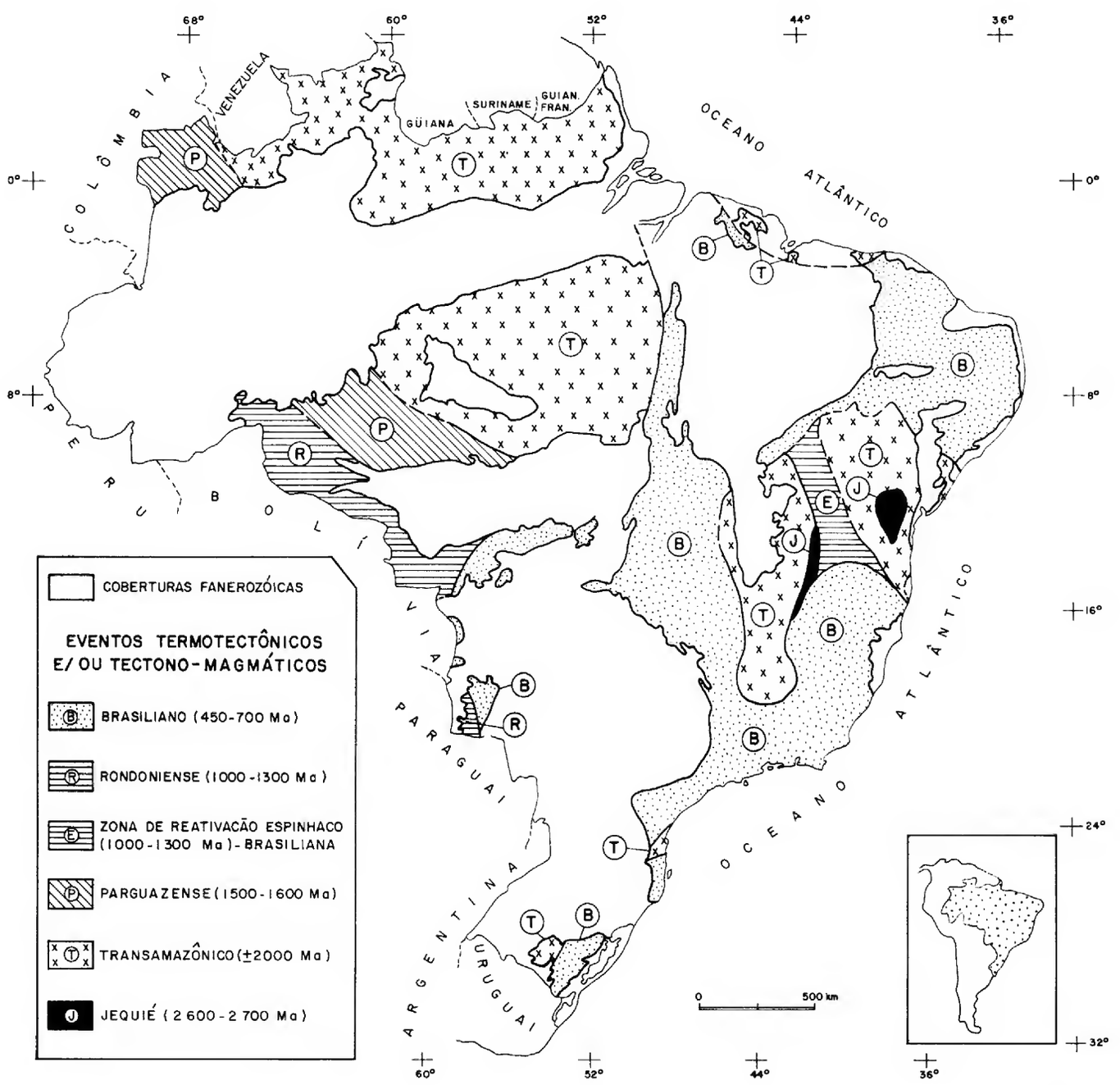


Figure 2.32. Positions and ages of the ancient (Precambrian) platforms (shields, highlands) of Brazil. From Schobbenhaus et al. (1984). Used with permission of Ministério das Minas de Energia, Departamento Nacional da Produção Mineral, Brasília, Brazil.

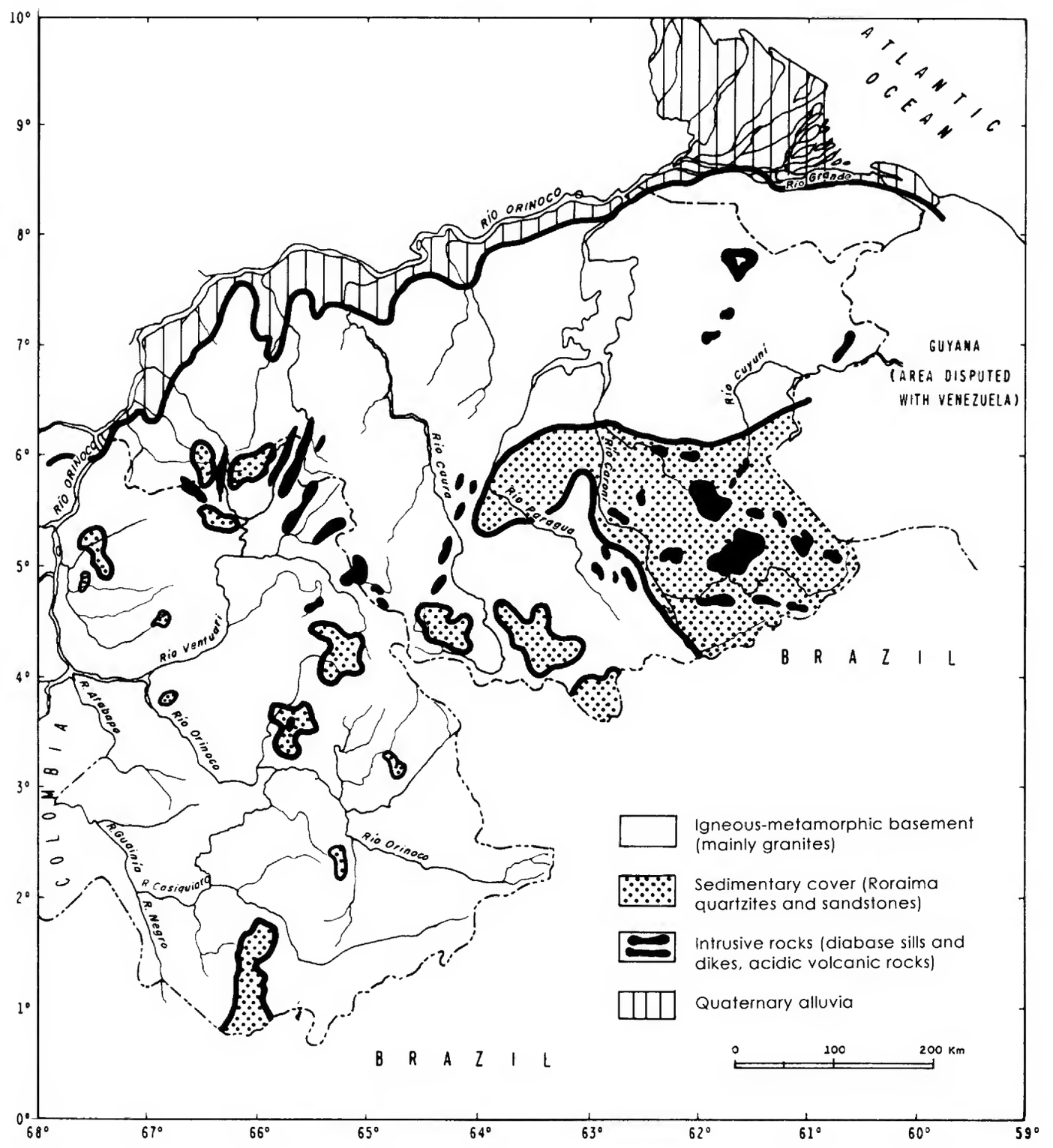


Figure 2.33. Simplified geologic map of Venezuela. From Huber (1995). Used with permission of Missouri Botanical Garden, St. Louis/Timber Press, Portland, Oregon.

America (U.S. Geological Survey Central Energy Team, 1999; http://energy.cr.usgs.gov/oilgas/wep/index.htm [one menu choice is World Geologic Maps]). For the Quaternary, there are summaries by Clapperton (1993) and Williams and Ferrigno (1998). Maps and geologic treatments for individual countries include those for Bolivia (Servicio Geológico de Bolivia, 1968; Marsh et al., 1995), Brazil (Schobbenhaus et al., 1984, including reproductions of geologic maps from 1854 to the present), Chile (Frutos, 1986a, b; Frutos et al., 1986), and Uruguay (Preciozzi et al., 1980; Ford et al., 1990). There is also an overall review of the geology of the Andes by Zeil (1979) and a coal map of South America (Weaver & Wood, 1994) that facilitates research on Tertiary vegetation through palynology by providing the location of coal deposits.

The Northern Shields and Highlands, Tepuis, and Basins (Fig. 2.32)—The oldest rocks in northern South America belong to the Imataca complex of the Guayana Highlands of Venezuela (Figs. 1.35, 2.33). They are dated at 3+ Ga and, along with the Brazilian Highlands, are part of the original cratonic platform on and around which the other physical features of South America were formed. Where the crystalline shields have been exposed to prolonged weathering, they form rocks with a sugarloaf texture and soils of low water-holding capacity as in portions of eastern Brazil. This edaphic condition augments the low annual rainfall (500 mm in places and less in El Niño years), meager atmospheric moisture from low rates of transpiration, and high albedo (heat reflectivity), contributing to the formation of dry cerrado and caatingas vegetation.

Flexuring of the cratonic surface and collapse of some portions over the past 600 Ma have produced the great downwarped lowlands of the Amazon Basin (Putzer, 1984), now filled with more than 4000 m of sediment, and the lowlands of the Orinoco, Paranaíba–São Francisco, and Paraná rivers (Fig. 2.34). The Amazon Basin is an intercratonic depression located on the Brazilian Shield. Continental sediments of Paleozoic, Mesozoic, and Paleogene age in the basin were derived from erosion of the Brazilian and Guayana shields (e.g., the 1.6 Ga Roraima Group; Gibbs & Barron, 1993, p. 119; the Middle Cretaceous Alter do Chão Formation). Erosion of Roraima quartzites and sandstones also produced the distinctive tepuis of the region (Figs. 1.41, 2.35; U.S. Geological Survey & Corporación Venezolana de Guayana, Tecnica Minera, C.A., 1993).

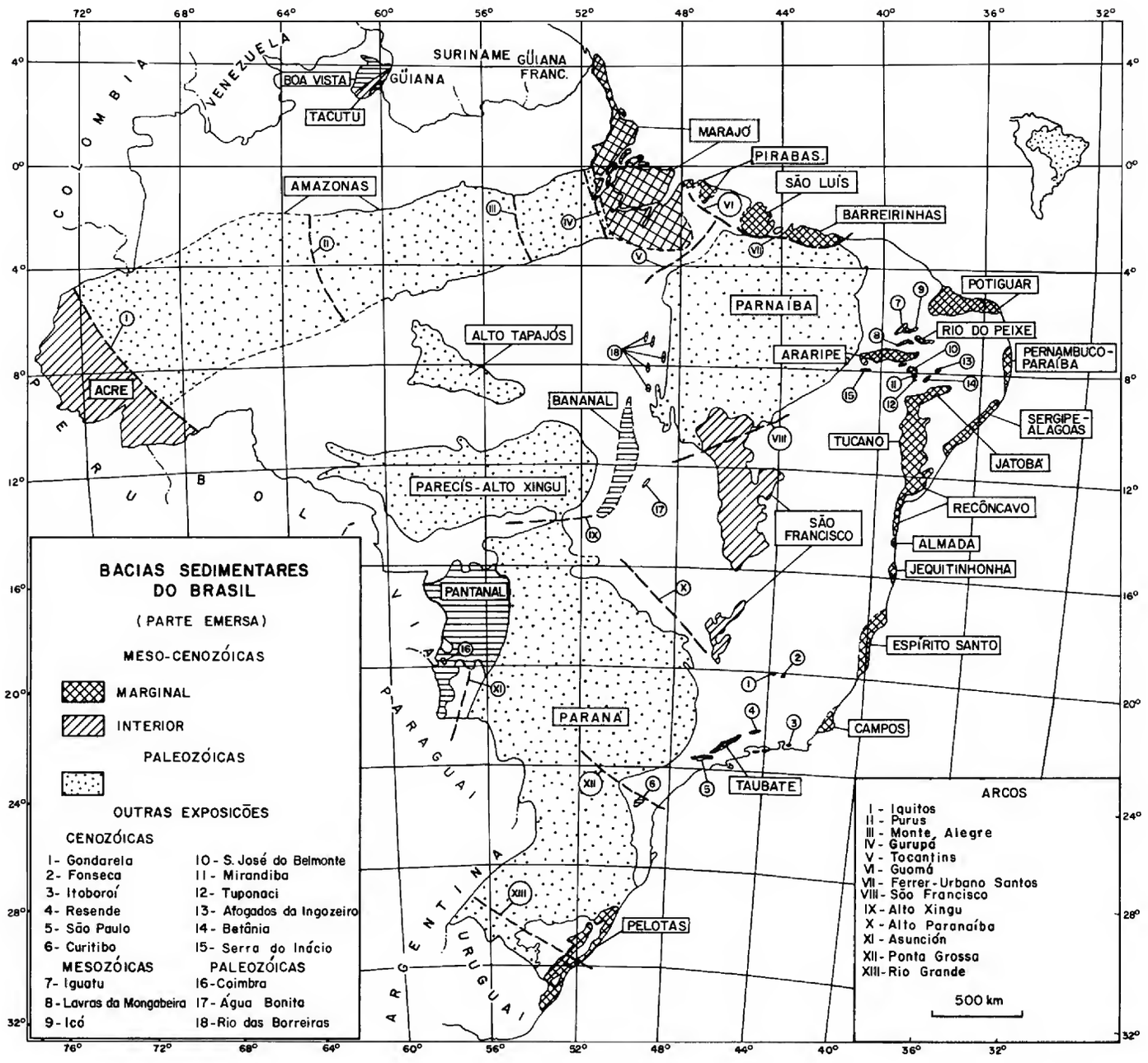


Figure 2.34. Positions and ages of the sedimentary basins of Brazil. From Schobbenhaus et al. (1984). Used with permission of Ministério das Minas de Energia, Departamento Nacional da Produção Mineral, Brasília, Brazil.

Marine beds were first deposited in the upper Amazon Basin from Pacific Ocean waters extending from the west prior to the rise of the Andes Mountains. The Rio Acre Formation of Maastrichtian age is one such unit, and similar deposits are known from the Oriente of Ecuador and from eastern Peru. Marine incursions from the newly opening Atlantic Ocean later deposited Cretaceous sediments into the lower Amazon Basin from the east (Marajó Formation). At the Cretaceous–Tertiary boundary in the Poty Quarry section near Recife, Pernambuco, Brazil, there are tsunami deposits, associated with iridium concentrations 69 times the background levels, resulting from the asteroid impact at Chicxulub, Mexico (Albertão & Martins, 1996). From about the early Miocene onward, the Amazon Basin received additional sediments from increasing erosion of the rising Andes Mountains.

Cores reveal fluctuating lowland swamp, lagoon, and fluvial conditions in the Amazon Basin throughout the Tertiary. For example, in the early and middle Miocene (23–12 Ma) there were marine incursions into the upper Amazon region from the Caribbean Sea through the Maracaibo Basin resulting from changes in sea level, tectonic movements, and downwarping of the Amazon Basin from the accumulating erosion sediments (Hoorn et al., 1995). The setting has been interpreted as a marine seaway extending across the entire basin with sediments being derived primarily from the Guayana Shield (Räsänen et al., 1995). However, Vonhof et al. (1998) believe on the basis of strontium isotope ratios and the strontium content of mollusks from the Pebas Formation (middle to late Miocene), that the western Amazon Basin was predominately a freshwater swamp-lake receiving runoff from the Andes Mountains, and that marine influence was periodic and confined mostly to the basin margins. Recent sedimentological and fish faunal evidence support this interpretation. Campbell et al. (2006) envision a mega-Lago Amazonas, or more likely a series of connected

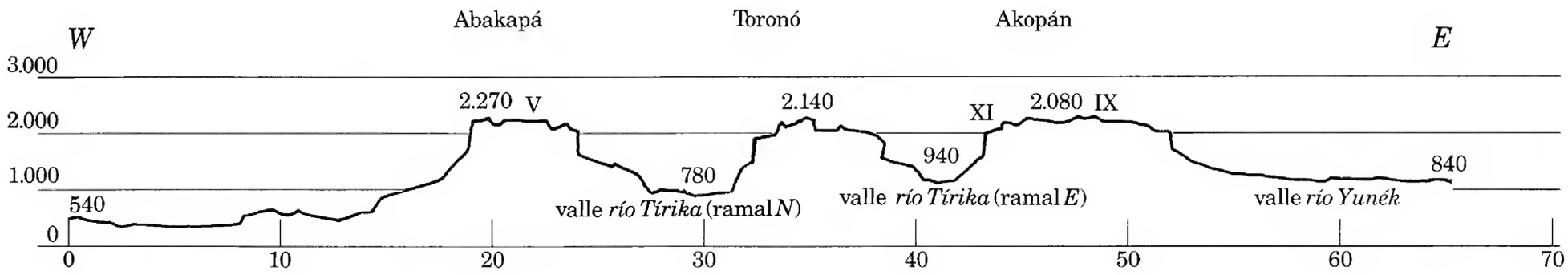


Figure 2.35. Topographic profiles of tepuis, Chimantá region, Venezuela. From Huber (1992). Used with permission of Otto Huber.

Figure 2.36. Interbedding of slates (metamorphosed shale) and quartzites (metamorphosed sandstone) in the Paleozoic of the Cordillera Real of Bolivia. From Zeil (1979). Used with permission of Gebrüder Borntraeger, Berlin, http://www.borntraeger-cramer.de.

mega-lakes, covering most of the Amazon Basin from the latest Miocene (~9.5 Ma) to the latest Pliocene (2.5 Ma) when the modern Amazon River drainage was established (as opposed to the late Miocene). In the late Miocene, the Maracaibo River emptying into the Caribbean Sea was dammed by uplift of the Eastern Cordillera to form Lake Maracaibo with 7000 m of sediment. There are volcanic ash deposits in the southwestern Amazon Basin of eastern Peru that contain paleofaunas dated at 9.01 and 3.12 Ma (Campbell et al., 2001). The latter date marks the last marine incursion into the region.

There are usually biological consequences associated with major changes in the physical environment. The Amazon Basin has the greatest number of freshwater fish species in the world, and Lovejoy et al. (1998; see also Lovejoy et al., 2006; Albert et al., 2006) believe on the basis of molecular phylogeny of the stingrays that this diversity involved the repeated isolation of marine species by fragmented freshwater habitats following periods of marine incursion. This is the kind of mechanism envisioned by Haffer (Chapter 8, Refugia) as operating in the Quaternary and contributing to diversity in other groups. In the late Miocene, shallow marine waters also extended southward along the Llanos–Chaco–Pampa Depression (Paraná Formation). These deposits cover red evaporite deposits of gypsum, and the sequence reveals fluctuating dry and humid intervals throughout much of the Cenozoic. It is biologically relevant that the dry intervals correlate with cold periods (glaciation in the Northern Andes Mountains; Iriondo, 1999), providing an example of the frequent but not inevitable association of cool climates and dry conditions in the lowlands. This association is an issue in some biodiversity models proposed for the Neotropics in which the Amazon Basin of the Quaternary is considered cooler than at present but not sufficiently dry to disrupt the moist forest during glacial intervals. The fluvial (river) and lacustrine (lake) deposits in the basin include bands of lignites, such as those in the Pebas or Iquitos Beds near the Brazil–Peru border, and these are potential sources of plant microfossils.

As a result of the rising Andes Mountains, narrow folds were produced in the floor of the Brazilian Amazon Basin, such as the Iquitos, Purus, and Gurupá arches. Many of these are obscured by more recent sediments, but when they formed they fragmented distributions, and while they were fully exposed they constituted barriers to the migration of some organisms. Evidence of these effects is still preserved as molecular differences among morphologically similar and presently contiguous rodent populations, but located on either side of ancient barriers such as the Iquitos Arch (Chapter 8, The Many Faces of Biogeography).

An example of the interaction between geologic structures, vegetation, and climate comes from the wetlands presently covering about 20% of the Amazon Basin. Their boundaries are often fixed by fault lines that define hydrological patterns. In turn, the wetlands are a significant source of methane. Thus, faulting contributes to the formation of wetlands that generate methane, which is an important climate-regulating greenhouse gas (Forsberg et al., 2000).

During the Quaternary at the LGM 18 Kya, sea level was lower than at present by about 120 m, and fluctuations in water depth across the lowermost Amazon River region (Vital & Stattegger, 2000) were augmented by epeirogenetic events (slight upward or downward movement of land surfaces usually without extensive folding or tilting). This resulted in frequent and extensive episodes of ponding, like the slower-paced ones of the Tertiary, the formation of many large lakes, and erosion that etched terraces into sediments 30–180 m above present sea level. These are evident, for example, on Marajó Island at the mouth of the Amazon River (Klammer, 1976, 1984). To the northeast, on the Campos de São Francisco of Brazil, there is also evidence from sediment analysis of late Pleistocene to Holocene tectonic activity (Modenesi-Gauttieri et al., 2002).

To the south in the Pampean region the Rosario Formation includes loess sediments (wind-blown; dry conditions) inter-

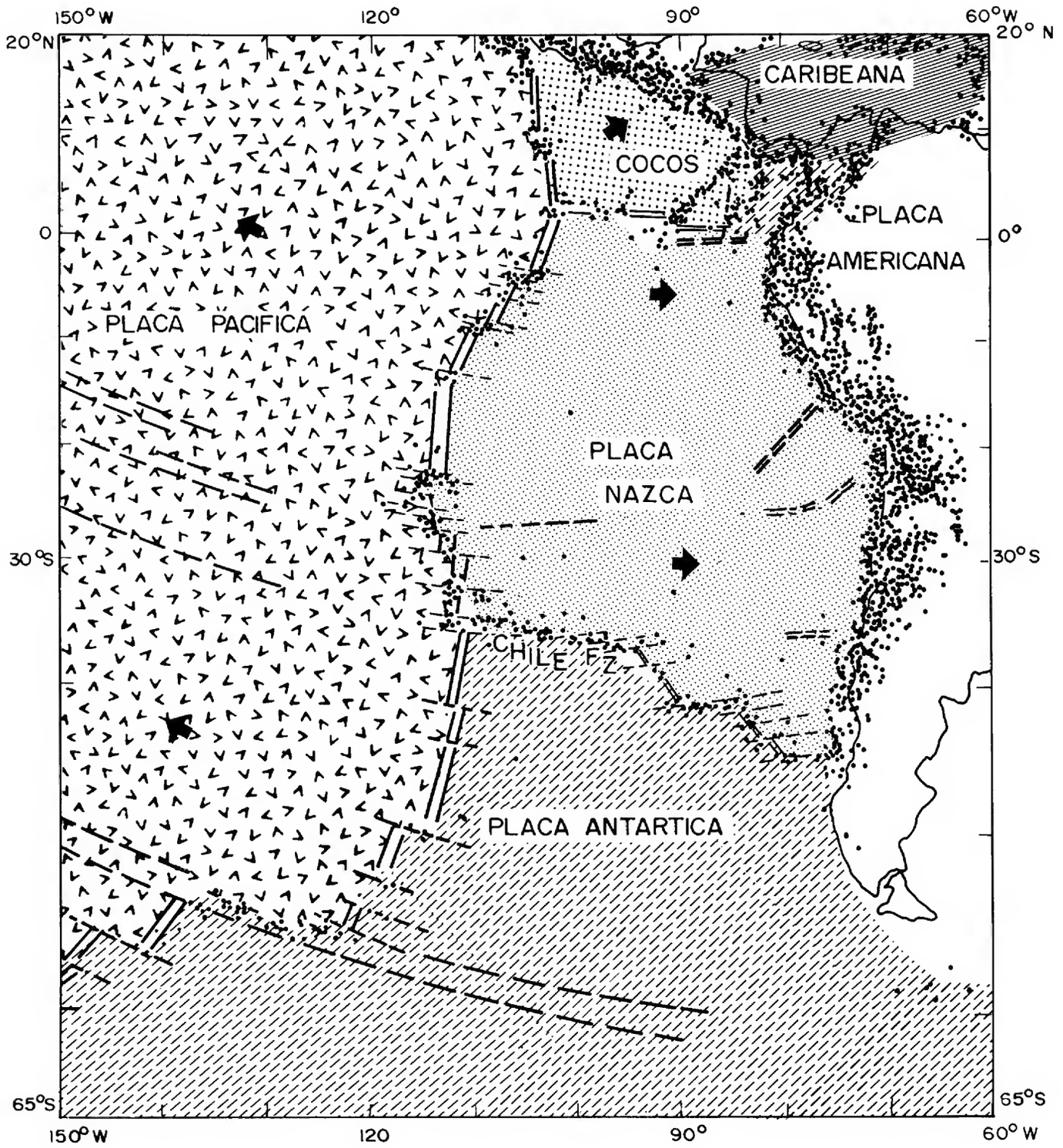


Figure 2.37. Tectonic plates influencing the geologic development of the Andes Mountains. From Frutos (1986b) in Frutos et al. (1986). Used with permission of Editorial de la Universidad de Concepción, Concepción, Chile.

calated with silt deposited in expanding swamp environments (moist conditions). The sediments can be dated at 0.73 Ma because the Brunhes–Matuyama magnetic reversal boundary is located in the upper part of the formation (I: p. 98). In the Entre Ríos region, the Hernandarias Formation covers most of the province and includes aeolian deposits (dry conditions). Hydrological analyses indicate that during its deposition rainfall was about 13% of the present, or ~100–150 mm/yr. The Hernandarias Formation is between 1.3 and 0.8 Ma. These lines of evidence document a dynamic physical environment in lowlands of South America in the Quaternary involving cycles of wet and dry climates beyond times included in available pollen diagrams.

The Northern Andes—Gansser (1973) first proposed the three orogenic provinces now recognized for the cordillera of South America—the northern, central, and southern Andes Mountains. The western margin of the craton provided the core of the mountains composed of folded Precambrian igneous and metamorphic rocks 1.80 to 1.18 Ga. Intrusion of Paleozoic rocks (Fig. 2.36) and deformation in the Early to Middle Jurassic (~180 Ma) resulted from the westward movement of South America. By the Late Cretaceous, the connection between the Amazon Basin and the Pacific Ocean was restricted by uplift of portions of the early low-lying Andean system, but limited connections were maintained through passes along which the proto-Amazon and Orinoco rivers drained into the Pacific Ocean. In the Cretaceous and Paleocene, there were still basins receiving marine sediments along the present site of the Andes Mountains (Sempre et al., 1997). The Pacific Ocean–Amazon Basin connections were maintained until about the middle Miocene (~15 Ma) when the Andes Mountains reached heights sufficient to become an effective barrier between the two provinces, and the lowlands were tilted eastward. Between 15 and 8 Ma, the Amazon and Orinoco rivers began to flow into the Atlantic Ocean, forming the vast alluvial and delta deposits that now spread across the northern margin of South America (Potter, 1997). That the Northern Andes and the northern part of the Central Andes had reached heights to determine the broader drainage patterns in the Amazon lowlands by the middle Miocene (~15 Ma) is clear from several independent lines of evidence. For example, van der Hammen (1952), Hoorn (1994a, b), and Hoorn et al. (1995) describe a change from west-dipping cross bedding in the early to middle Miocene (Mariñame unit), to east-dipping

cross bedding in the middle to late Miocene (Solimões and Pebas formations) along the Solimões River. At the mouth of the Amazon River, a submarine fan first appears in the middle Miocene, and river-transported deposits of the same age begin to appear offshore along the Guianas.

In contrast to the ancient shields and basins, other physical features of northern South America had their origins more recently in Cretaceous and Cenozoic times through deformation, subduction, and accretion of allochthonous (exotic or transported) blocks added along the northern and western coasts of the platforms (Case et al., 1990; Clapperton, 1993; Ramos, 1999; Figs. 2.37, 2.38). In the Late Cretaceous, what would eventually become the Cordillera Occidental was accreted onto northwestern South America (Winsemann, 1994) as indicated by the presence of ophiolites. The suture is represented by the Romeral Fault Zone (upper arrow in Fig. 2.38), which is a major feature at the western contact between the Caribbean and South American plates. Much of the uplift of the non-volcanic Northern Andes Mountains (Cordillera Central and Cordillera Oriental) resulted from oblique subduction of the Nazca Plate, presently at a rate of ~3.1 cm/yr and moving N–NE on a bearing of ~80°, and the southern movement of the Caribbean Plate in the Miocene, by which time the Northern Andes Mountains had attained about one-half their present average elevation. The pulsating nature of the uplift produced cycles of subsidence and deposition followed by uplift and erosion. For example, the uplift of the Eastern Cordillera of Colombia to its present height occurred between 6 and 3 Ma. The High Plain of Bogotá is the floor of a former lake basin that formed

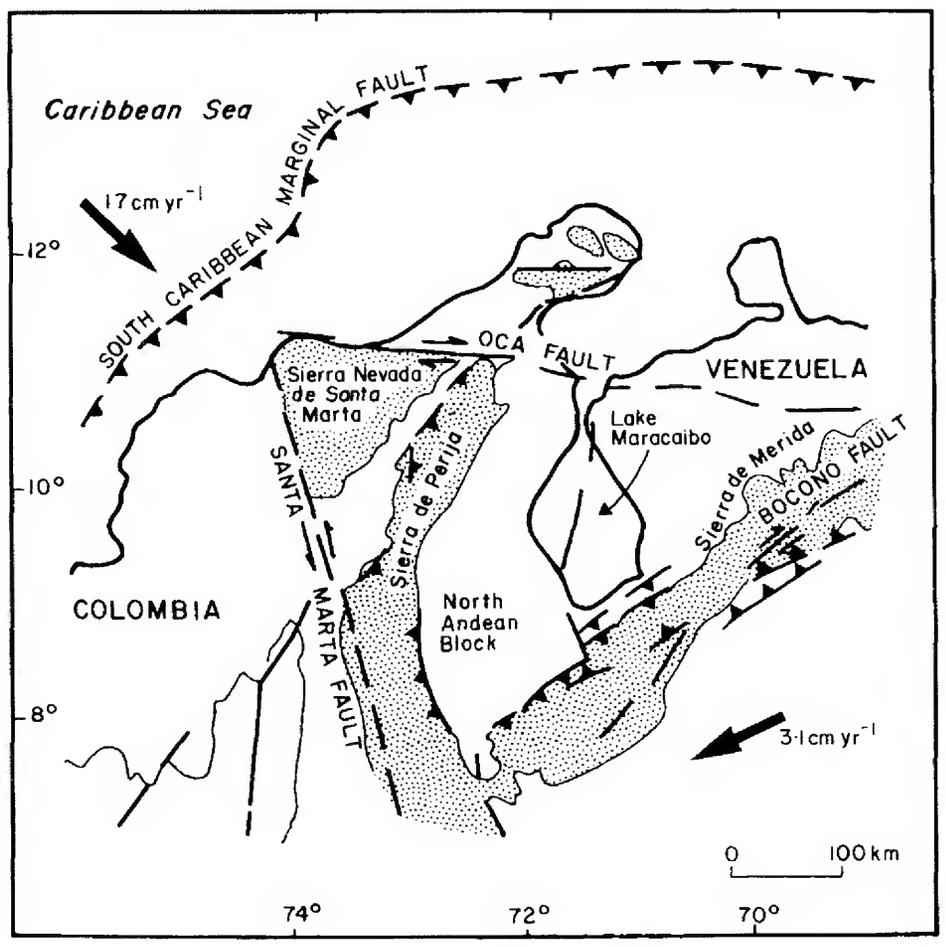


Figure 2.38. Northern Andean Block and interactions between Nazca and Caribbean oceanic plates with the South American continental plate. The area bounded by the Santa Marta, Oca, and Bocono faults defines the northern Andean Block. Reprinted from Clapperton (1993) with permission of Elsevier Science Publishers, Amsterdam.

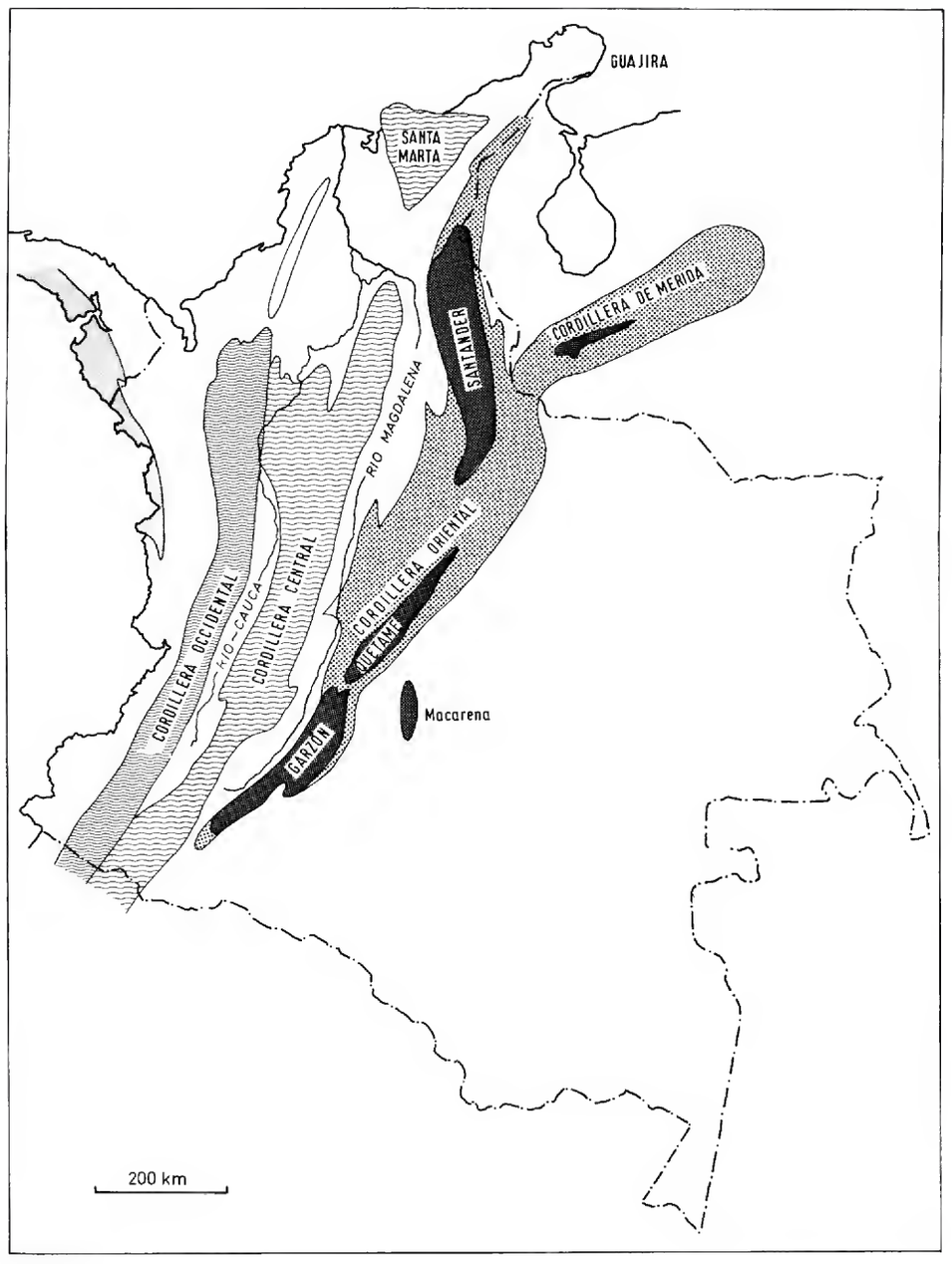


Figure 2.39. The Venezuelan and Colombian Andes Mountains and valleys of northwestern South America. From Zeil (1979). Used with permission of Gebrüder Borntraeger, Berlin, http://www.borntraeger-cramer.de.

~6 Ma when the cordillera underwent a period of major uplift. The basin was further elevated to 2550 m at ~4–3 Ma. Sedimentation was nearly continuous until 25 Kyr, when the southeast part of the basin was breached, leaving the present flat plain containing more than 700 m of lacustrine fossil-bearing material.

The Guajira Peninsula–Sierra Nevada de Santa Marta Block is one of several allochthonous terranes that formed through convergence of the South American and Caribbean plates. The Santa Marta Mountains are the highest in Colombia at 5800 m. The Cordillera Occidental and the eastern part of Panama were accreted and uplifted by convergence of the Caribbean, South American, and Nazca plates. This region is especially complex because collision of numerous small blocks has brought together crustal fragments of different origins. The initial rise of the Central Cordillera through accumulation of volcanic rocks occurred in the Oligocene (Villamil, 1999; Mann et al., 2006). The central, western, and eastern cordillera (highest block is the Sierra Nevada del Cocuy at 5493 m) of northern Colombia, the Sierra de Perijá at the Colombian–Venezuelan boundary (3650 m), and the Cordillera de Mérida of Venezuela (4000 m) were further uplifted in Miocene and Quaternary times. It is estimated that the Sierra de Perijá was uplifted at a rate of

~11–16 mm/yr during the Quaternary. Clapperton (1993, p. 34) notes that "terminal moraines of the Last Glaciation in the Mérida Andes have been offset several tens of metres by right-lateral slip, demonstrating that tectonic movement has continued during the Holocene. Thus, it is possible that some parts of the Northern Andes are now more than 1,000 m higher than they were at the start of the Quaternary, assuming only a modest amount of lowering through denudation."

To the west, across northern Venezuela to Trinidad and Tobago, there is a series of over-thrusted structures called nappes (French for "covers" or "stacked sheets"). The distinctive nappe structures of northern South America are composed mostly of Jurassic and Cretaceous rocks obducted onto the continent in the latest Cretaceous as a result of compressive interactions of the South American and Caribbean plates mostly in the Middle Tertiary. The islands off the north coast of Venezuela are of similar age and represent peaks of an island arc chain called the Caribbean Mountain System. Among these, the Netherland Antilles emerged in the Miocene and the Las Aves and associated islands appeared in Recent times. Continuing compression of the plates produces the mud volcanoes that are a feature of the Orinoco Delta, where underlying Miocene and Pliocene mud and clay are forced upward along faults (Aslan et al., 2001).

The Northern Andes consist of two structurally defined geomorphic subprovinces. The northern Andean Block extends from the Caribbean Plate to a structure called the Bahia Solano–Macarena megashear across southern Colombia (2°4'N). It formed in the late Miocene–Pliocene when the Panama volcanic arc, moving N–NE along the East Andean–Boconó Fault Zone at 6–9 mm/yr (Mann et al., 2006), collided with northern South America. Here the Nazca Plate descends beneath northwestern South America, and the Cordillera Central of Colombia has emerged as a result. In contrast to the volcanic mountains of the northern Andean Block, these mountains are accreted in origin. The eastern, central, and western cordilleras of Colombia topographically merge in southern Colombia where the Carnegie Ridge, a submarine mountain range more than 3000 m in height on the Nazca Plate, begins to descend into the subduction zone. It formed over the Galápagos hot spot and began subducting beneath southern Colombia–Ecuador in the Pliocene (~3.2 Ma).

The other subprovince extends from the northern Andean Block to a feature known as the Amotape Cross at 5°S in southern Ecuador and northern Peru near the Golfo de Guayaquil. This is another megashear feature representing a more ancient contact between segments of the South American Plate. In Ecuador, westward movement of South America and subduction of the Nazca Plate accreted Paleozoic and Early Cretaceous terranes onto the coast during Late Cretaceous through Eocene times, and elevated the eastern Cordillera Real and the western Cordillera Occidental volcanic ranges, separated by the Central Valley or Interandean Depression (Fig. 2.39). In the early Miocene, the Pacific Ocean extended into the present Oriente region of Ecuador, in the middle Miocene the Eastern Cordillera was uplifted, and the Central Valley developed in the early Pliocene from lateral spreading resulting from the uplift of the eastern and western cordilleras. Continuing uplift has raised blocks in the Ecuadorian Andes ~150 m in the past 7000 years.

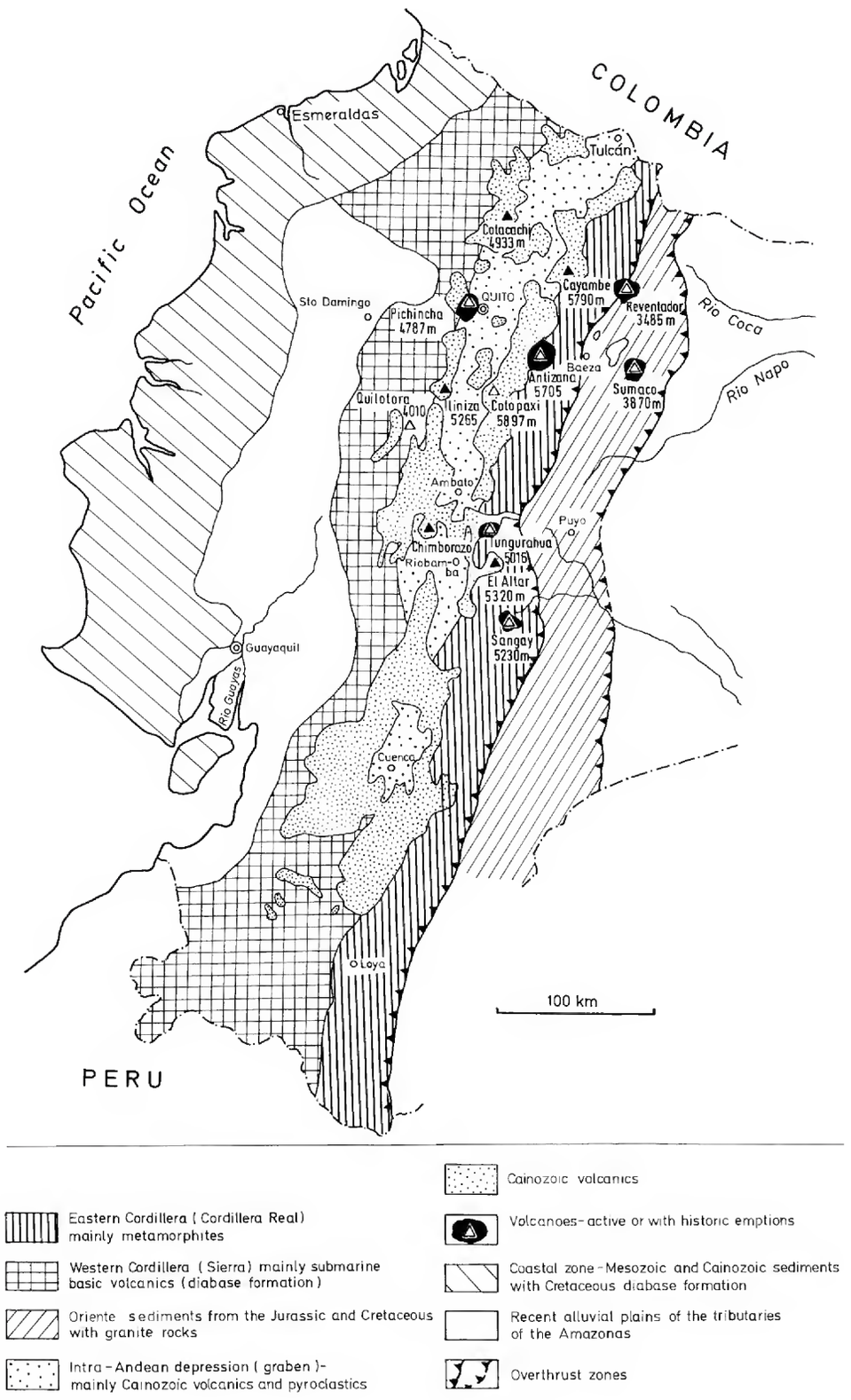


Figure 2.40. Tectonic elements of the Andes Mountains of Ecuador. From Zeil (1979). Used with permission of Gebrüder Borntraeger, Berlin, http://www.borntraeger-cramer.de.

The Central Valley in northern and central Ecuador contains a rich late Pleistocene mammalian fauna in the Cangahua Formation. That assemblage records the disappearance of mastodonts from Ecuador and fluctuations in the abundance of mylodonts and equids, with increasing cold and aridity at the LGM (Ficcarelli et al., 1997; Coltorti et al., 1998). There is a general summary of Andean geology by Sauer (1965, in Spanish; 1971, German translation), and there are recent reviews of the Ecuadorian Andes by Coltorti and Ollier (2000) and of the Neogene geology of southern Ecuador by Hungerbühler et al. (2002). A work of historic interest on the geology of the Ecuadorian Andes Mountains by Wolf (1892) was reprinted and annotated in 1975.

The Central Andes—The Central Andes extend from the Amotape Cross (5°S) to the Golfo de Penas (46°S) in southern Chile at the contact between the Nazca and Antarctic plates. South of the Nazca Ridge (~15°S), the Peruvian Andes Mountains reach an elevation of 5670 m at the Quelccaya summit. This is where ice cores drilled by Lonnie Thompson have contributed so significantly to revising the earlier presumed stability of tropical climates (Kennan et al., 1995; Krajick, 2002; Cordillera Oriental; see below and Chapter 7).

The Bolivian part of the Central Andes Mountains has been extensively investigated for scientific, military (i.e., the border dispute with Chile), and economic purposes. There are large deposits of copper, gold, silver, tin, and other minerals in the mountains, and the eastern lowlands have been explored for oil. The resulting geologic maps (Bolivian Geological Survey [GEOBOL] Geologic Map Series 1:100,000), seismic profiles, aerial photographs, and satellite images have provided valuable information on the history of the Bolivian Andes. Lamb (2004) vividly recounts field experiences involved in obtaining the information. A digital geologic map of the Altiplano and the Cordillera Occidental is available at the USGS Geoscience Data Catalog Web site (http://geo-nsdi.er.usgs.gov/metadata/open-file/95-494/metadata.faq.html), and the general geology and mineral resources are discussed in a U.S. Geological Survey–Servicio Geológico de Bolivia (1992) publication with accompanying geologic map.

In Bolivia and Chile, the Andes Mountains reach their widest extent at 700 km and their highest average elevation at 4000 m with many peaks above 6000 m (Kennan et al., 1995). The mountains consist of three morphotectonic provinces that are, from the west, the Cordillera Occidental, the 250-km-wide Altiplano, and the Cordillera Oriental (Figs. 2.39, 2.40). These are mostly folded mountains augmented by volcanics and a few accreted terranes. Prior to the Pliocene, the area was especially active, probably due to the steep-angled slope (~35°) of the descending Nazca Plate. Volcanism decreased after ~5 Ma, probably due to lower-angle flat-slab subduction. However, some activity continues as shown by raised Plio–Pleistocene deposits near Antofagasta in northern Chile (Fig. 2.41). On 20 February 1835, Charles Darwin witnessed an earthquake at Valdivia, Chile, that elevated parts of the coast 3 m in a few minutes. On 22 May 1960, the largest earthquake ever recorded occurred near Concepción (magnitude 9.5), and there was a 7.8-magnitude earthquake in northern Chile on 30 July 1995. The uplift is estimated at a mean rate of 240 mm over the past 330 Kyr (Ortlieb et al., 1996). There has also been some volcanism during the past 930 Kyr along the coast of Chile (Singer et al., 1997). Darwin recorded a "great glare of red light" on 19 January 1835, which was the eruption of Corcovado Volcano in southern Chile (~42°S), inland from the Isla de Chiloé.

There are two principal forces generating orogenic and volcanic activity in the Bolivian Andes. One is subduction of the Nazca Plate along the volcanically active and overriding western margin of South America. This has produced subsurface magma and surface lava and accounts for about one-fifth of the height of the Cordillera Occidental. The other force is compression from the westward movement of the continent away from the Mid-Atlantic Ridge and against the Nazca Plate. This has folded and crumpled the western mountains and is responsible for about four-fifths of their height. Accelerated drift of the South American Plate after about 30 Ma has produced most of the elevation (Sobolev & Babeyko, 2005; Babeyko & Sobolev, 2005). The Atacama Fault runs along the western margin of the Cordillera Occidental where the mountain chain has broken along the trench of the Nazca Plate. Although it is a conspicuous geologic feature and slippage along the fault is responsible for many of the earthquakes, overall movement has been relatively slow and it has not played a major role in the rise of the Central Andes.

The very high altitude of the Central Andes is probably thermally induced due to a thinning of the lithosphere and buckling of the crust to great heights in the southern part of the Central Andes, such as the Ojos del Salado mountain system, which includes Cerro Aconcagua (32°S) at 6960 m in Argentina. A more speculative cause is that a portion of the root of the mountains may have become detached through subduction, creating a rebounding rise of the unanchored cordillera (Lamb, 2004).

Figure 2.41. Recent uplifted Plio–Pleistocene sediments near Antofagasta, northern coastal Chile. From Zeil (1979). Used with permission of Gebrüder Borntraeger, Berlin, http://www.borntraeger-cramer.de.

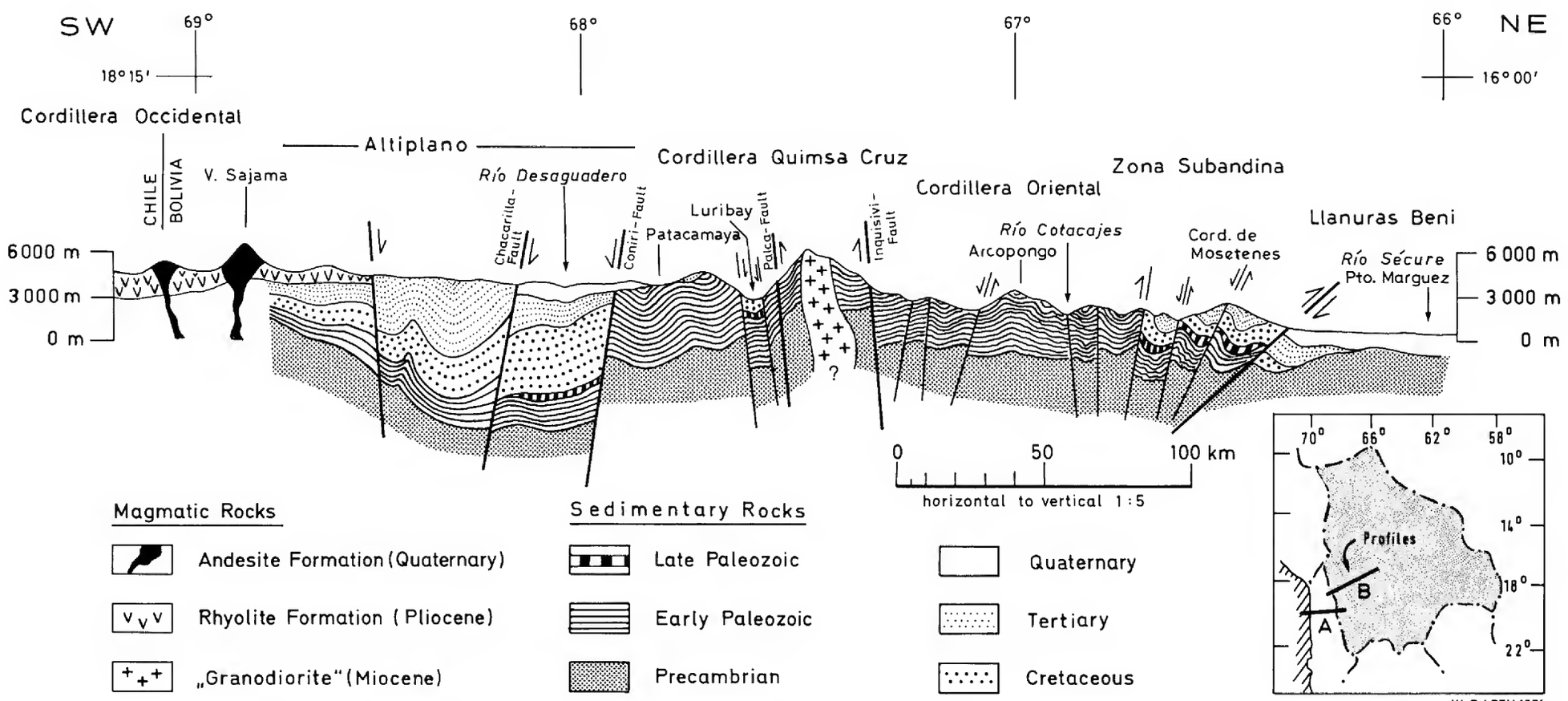


Figure 2.42. Sectional view of the Bolivian Andes Mountains showing approximate elevations, faults, rock types, and ages in the Cordillera Occidental, Altiplano, and Cordillera Oriental. From Zeil (1979). Used with permission of Gebrüder Borntraeger, Berlin, http://www.borntraeger-cramer.de.

After great heights are attained by mountain systems, additional forces are required to sustain the exceptional elevations (Lamb & Davis, 2003). Most high mountains result from the collision of two plates (e.g., the Asian and Indian plates at about 4 cm/yr with the uplift of the Himalayas). Contacts that involve the subduction of one plate (e.g., the Nazca Plate) beneath another (the South American Plate) typically do not produce such great elevations. Estimates are that if compression of the western edge of the South American Plate against the Nazca Plate were the only factor, the Andes Mountains would be ~2 km in average elevation rather than their present 4 km. If, however, the sliding of the Nazca Plate beneath the South American Plate were impeded by lack of lubricating sediments eroded from the mainland, slower subduction and the buildup of friction would sustain much higher mountains. Lamb and Davis (2003) suggest the following sequence of events: there is reduced evaporation of water from the surface of the cold Humboldt Current, little rain is produced, there is minimal erosion and few or no major rivers to transport lubricating sediments into the South American Trench, subduction is impeded, compression forces increase, and sustained high mountains result.

The Cordillera Oriental are folded and faulted mountains that also result from the relative eastward push of the Nazca Plate. Rather than this pressure being partly absorbed by subduction, however, the eastern mountains are being compressed against the Brazilian Shield. The Andes Mountains moved more than 100 km eastward between approximately 30 and 20 Ma (middle Oligocene to middle Miocene), and another 100 km in the past 10 Ma. The Eastern Cordillera is now riding up and over the western margin of the Brazilian Shield, producing great heights and the characteristic corrugated topography of the Yungas described in Chapter 1.

The Altiplano has a mean elevation of 3700 m (Chapter 1, Bolivia). It is structurally a series of high, intermontane fault-bounded basins between the Cordillera Occidental and Cordillera Oriental and filled with up to 10 km of Tertiary terrestrial sediment.

The sinuous course of the Andes Mountains is a result of different intensities in the compression forces operating along their length. The strongest forces are exerted in the central sector where the Andes Mountains bend sharply to the west (the Bolivian Orocline, or "elbow" of the Andes with Cochabamba near its center). The Andes Mountains did not form by following a curved continental platform. Rather, they were originally more north-south in orientation, and the strength and inexorable pressure on the heated and relatively fluid rocks bent the mountain chain into its present configuration within the last 10 Ma.

Timing—The Central Andes Mountains had their beginnings near the end of the Cretaceous when the region along the western coast of South America was a large swampy lake or inland sea. This is shown by the original, mostly undeformed horizontal layering of the Cretaceous strata without interbedded layers of eroded sediment. The Cretaceous limestones of Bolivia preserve one of the largest concentrations of dinosaur footprints in the world. Nearby to the west in the Pacific Ocean, there was a line of isolated volcanoes that contributed some lava and volcanic ash, and that later would play an important role in the construction of the Central Andes Mountains.

At ~40 Ma, a layer of eroded sandstone and siltstone was deposited over the Cretaceous sediments, indicating the presence of uplands in the adjacent region. Occasional latest Cretaceous–early Paleocene deformation documents some up-

lift at that time (Fig. 2.42). This is later than to the south and earlier than to the north (Fig. 2.43), as shown by the age of fluvial basin deposits (Potter, 1997) and consistent with the south to north opening of the Atlantic Ocean. In the middle Paleocene, there was some limited sediment accumulation in the fore-arc basins (Horton et al., 2001). In the Eocene, there was rapid sediment deposition from uplift that deposited, for example, most of the Potoco Formation that contains a palynoflora from terrestrial plants of late Eocene to early Oligocene age (Chapter 7). Thus, a principal uplift of the Central Andes Mountains dates from the Eocene at ~40 Ma. Part of the reason for this timing is that at ~40 Ma, the convergence of the Nazca and South American plates slowed from ~15 cm to ~5 cm/yr. This was probably because the intensive collision of India with Eurasia at this time affected plate movement worldwide. As the plates along western South America slowed, then cooled from the reduced friction and hardened, the pressure on the continental margin from subduction increased.

The eroded sandstones and siltstones came from a low ridge rising from the former lakebed. By ~30 Ma, sediments were eroding from this ridge and being deposited as fans to the east and detritus that would eventually make up the Altiplano to the west. The original line of isolated volcanoes noted earlier had now coalesced into a more continuous chain of low mountains that would eventually constitute the Cordillera Occidental. At this time, the Altiplano was a river basin near sea level situated between the offshore, partly volcanic proto-Western Cordillera and the rising, mostly non-volcanic Eastern Cordillera. By the middle Miocene (15 Ma), about one-half (~2000 m) of the present high elevations (~4000 m) of the Eastern Cordillera had been achieved. This was sufficient to contribute to the development of fluctuating semiarid and arid environments to the west of the mountains as preserved in sequences of lacustrine deposits in the central Andean fore-arc region of northern Chile (Saez et al., 1999). Early to middle Miocene alluvial (river) deposits in Peru and Chile form the substrate of the present desert, indicating they were laid down before uplift of the mountains reduced rainfall. The trend toward aridity started in the middle Oligocene with the development of the Humboldt Current, which by the middle Miocene was cooling ocean waters globally. Hyperaridity is evident from sedimentological data at 4–3 Ma. The desiccating effect of the cold coastal waters beginning in the middle Oligocene, the uplift of the Andes Mountains sufficiently high to block moist winds from the east in about the middle Miocene, global cooling in the middle Miocene, and increased upwelling in the cold Humboldt Current with closing of the Central American seaway between 3.5 and 3 Ma combined to produced the Atacama Desert (Hartley, 2003). It was modernized in its extent and composition during the Quaternary, and it fluctuates with wet El Niño–dry La Niña events.

A mid-altitude paleocommunity of cloud forest at 3600 m elevation near Cochabamba, Bolivia (Fig. 2.44), shows the extensive uplift of the Eastern Cordillera during the past ~10 Ma. The present altitudinal range of cloud forest is 1200–1400 m, indicating an uplift of about one-half of the present average elevation since the late Miocene. Ghosh et al. (2006) used abundances of ^{13}C–^{18}O bonds in soil carbonates to estimate uplift of the Altiplano ~3700 m between 10.3 and 6.7 Ma. There is evidence of extensive Quaternary glaciation on the Puna in the form of cirques, moraines, tillites, striated rocks, hummocky surfaces, and salars, which preserve remnants of large glacial lakes. The Salar de Atacama at Antofagasta in northern Chile originated in the early Late Cretaceous from closure of a back-arc basin, and contains nearly 6000 m of red sandstone and evaporites (Mpodozis et al., 2005).

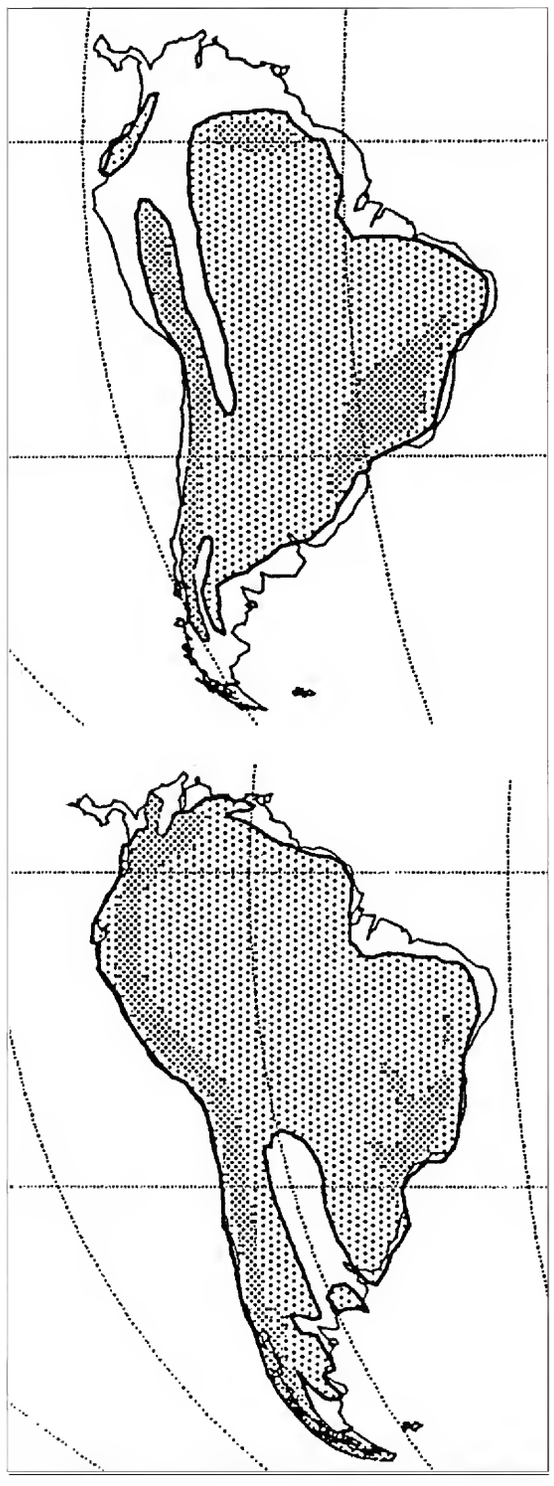


Figure 2.43. Coastlines of South America in the Cretaceous (Maastrichtian, 70 Ma, top figure) and in the late Miocene (Messinian–Tortonian, 19 Ma, bottom figure). White = ocean, light stipple = land of low elevation, darker stipple = land of higher elevation. From Smith et al. (1994). Reprinted with the permission of Cambridge University Press.

Pantanal—East of the Central Andes is the basin of the Paraguay River. Erosion sediments from the surrounding Brazilian Highlands, Mato Grosso Plateau, and the Andes Mountains have filled the basin with ~500 m of sediment averaging ~100 m in elevation. The alluvial fans of the Gran Chaco (see below) cover 40,000 km^2 in Argentina and eastern Bolivia and

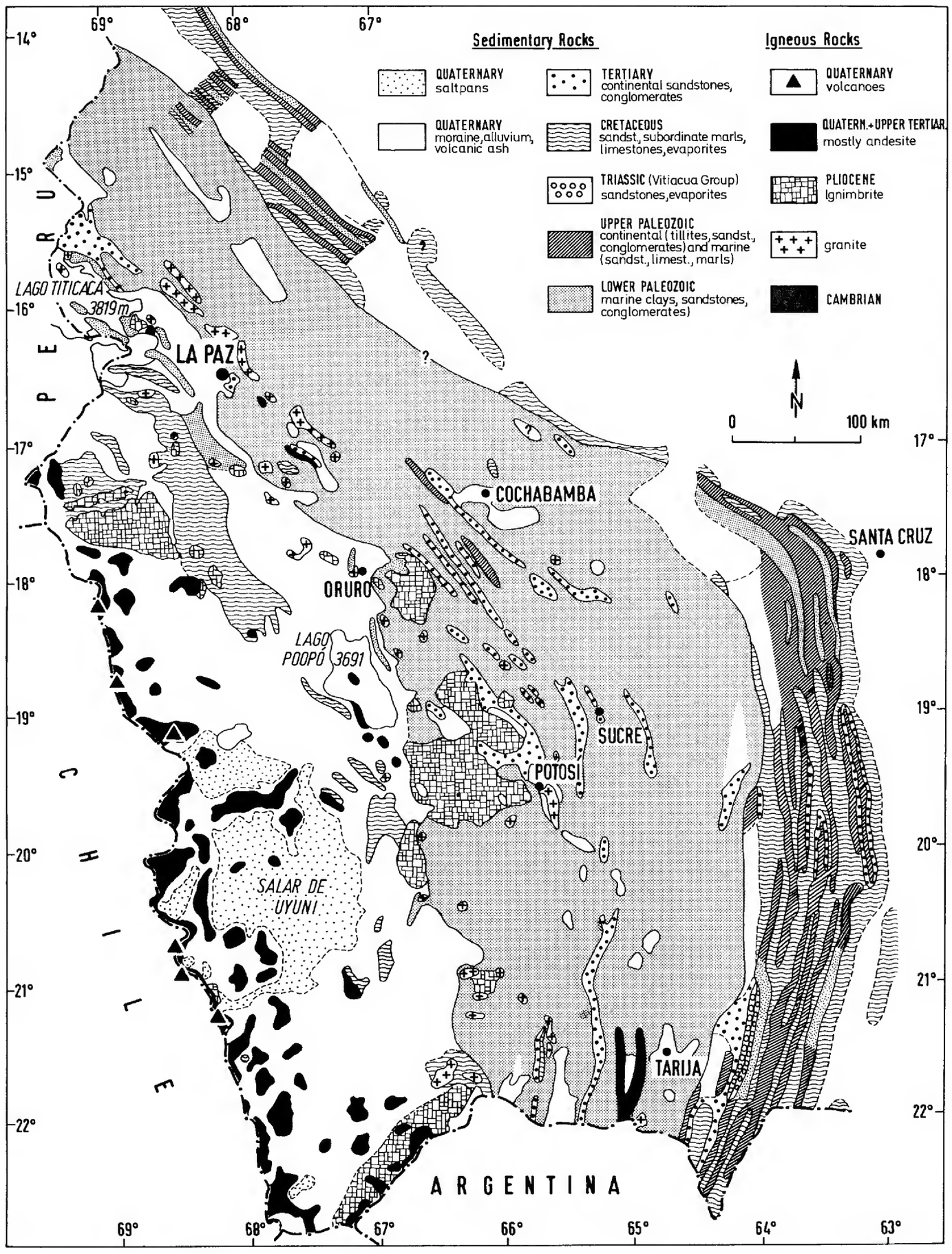


Figure 2.44. General geologic map of Bolivia. From Zeil (1979). Used with permission of Gebrüder Borntraeger, Berlin, http://www.borntraeger-cramer.de.

50,000 km^2 in southeastern Brazil. The latter is probably the largest alluvial fan system in the world, and it forms where the Taquari and Lourenço rivers descend from the Serra do São Lourenço Escarpment. The fans originated primarily during humid phases of the Pliocene and Quaternary. The Pantanal is a broad fault-bounded trough formed by subsidence of the Precambrian basement platform primarily in the Quaternary. The low-lying plains of the Pantanal are a mosaic of permanently inundated land intermingled with land that is covered only during the wet season. There are also uplands to ~600 m that represent erosion features and ancient deltas from older river system configurations. As noted previously, the Pantanal and Gran Chaco plains were probably connected to the sea during the Miocene through the Entre Ríos region as part of the Llanos–Chaco–Pampa Depression (Iriondo, 1999; Fig. 2.43, bottom figure; frontispiece, Chapter 1, South America). It was likely inundated and partially drained frequently during phases of uplift and subsidence and from sea-level changes associated with the warm-moist and cool-dry intervals of the late Cenozoic. Parts of the Pliocene were humid as shown by increased fluvial deposits from the Paraná River (Ituzaingó Formation). The pace of these changes undoubtedly quickened during the Quaternary.

Gran Chaco and Monte—South of the Pantanal along the eastern slopes of the Central Andes is the Gran Chaco of northwestern Argentina and its extension into Bolivia (the Chaco Boreal). It is an undulating alluvial plain covered with dry thorn woodland. The geology of the Salta Basin in northwestern Argentina is reviewed by Salfity and Marquillas (1994), and its history is representative of events and conditions along the eastern margin of the Central Andes Mountains (Malumián, 1999). Deposition in the basin began in the

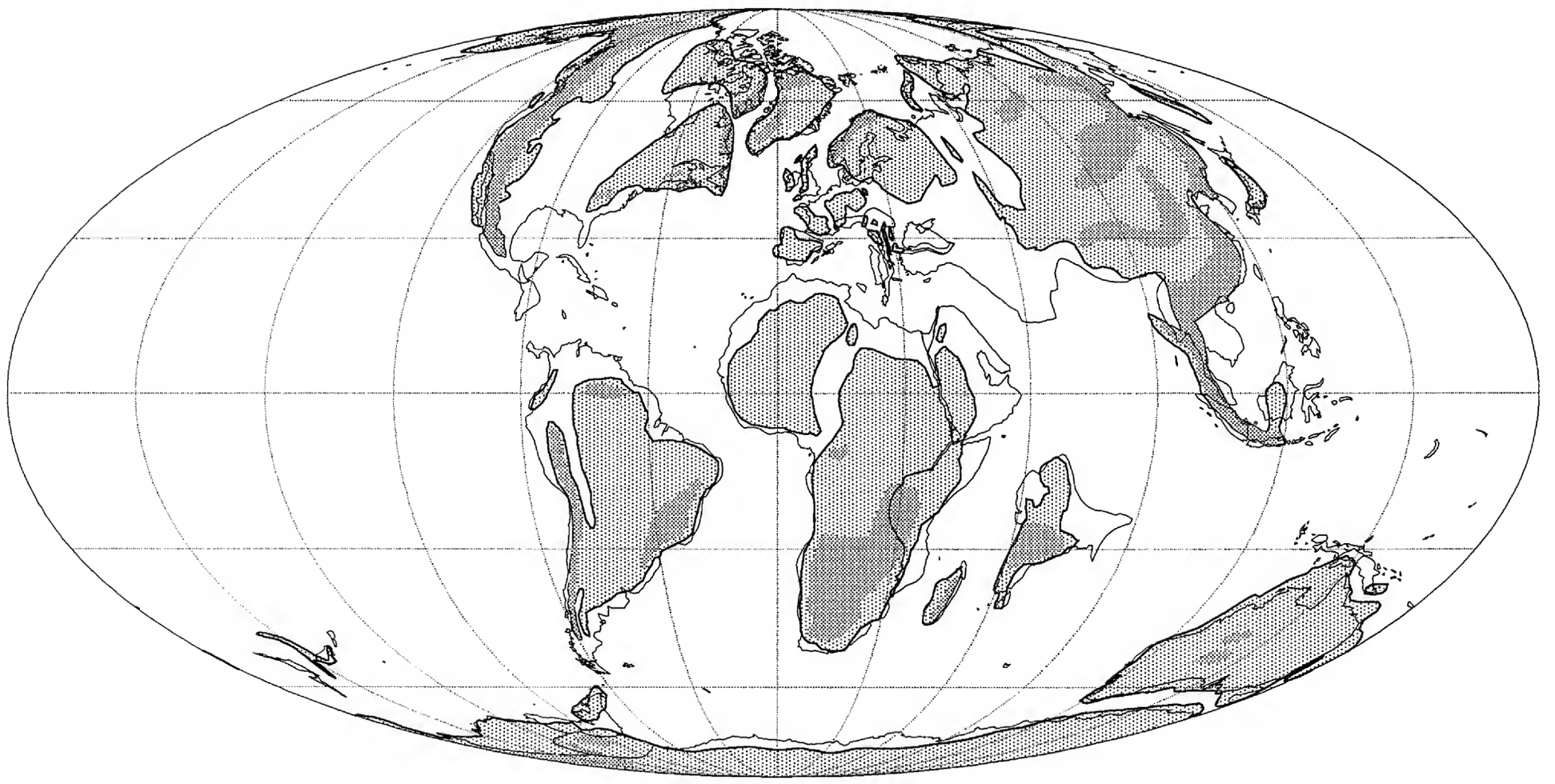


Figure 2.45. Global coastlines during the Late Cretaceous (Maastrichtian, 70 Ma). From Smith et al. (1994). Reprinted with the permission of Cambridge University Press.

Cretaceous with erosion sediments derived from the early Andes Mountains. These deposits constitute the Salta Group, which is divided into the Pirgua Subgroup of basal red beds (subaerial and dry conditions) of Cretaceous age deposited on the Precambrian–Paleozoic basement; the Balbuena Subgroup of sandstone, limestone, and shale of Campanian to Paleocene age; and the Santa Bárbara Subgroup of Paleocene to Eocene age. The Balbuena deposits are the result of a marine incursion into northwestern Argentina that was part of the high sea level characterizing the Cretaceous worldwide (Fig. 2.45). The inundation contributed to the termination of connections that had allowed the Early Cretaceous interchange of dinosaurs between North and South America (Bonaparte & Powell, 1980; Bonaparte, 1984). This ingression ended in Santa Bárbara as shown by the presence of terrestrial mudstones, lacustrine deposits, and red beds. Some tuffs document volcanism as ash settled onto lake surfaces. These were ideal conditions for the preservation of land and near-shore organisms across eastern and western Argentina, and the deposits are especially rich in Paleocene to Eocene mammals, reptiles, fish, insects, and plants (Pascual et al., 1981; Pascual, 1984; Quattrocchio & Volkheimer, 1990; Chapter 7). The Miocene inland sea from the Entre Ríos region, along the margin of the Pampas and into the lowlands of the Pantanal, extended into the Gran Chaco. The sea was shallow with restricted circulation based on the presence of evaporite deposits of salt and gypsum. Surface sediments are mostly river-deposited alluvium and include the alluvial fans noted along the eastern Andes Mountains into Paraguay, Bolivia, and southwestern Brazil. The slope and the relatively coarse nature of the geologic substrate and the derived porous soil contribute to the present dry vegetation of the Gran Chaco. In the late Quaternary at the various glacial maxima, and in the late Holocene, climates were dry as indicated by dunes and wind-blown loess sediments (Iriondo, 1993).

Farther to the south in western Argentina are the even drier upland valleys of the Monte region. Precipitation is lower than in the Gran Chaco, and in addition to the steep slopes and coarse soils, rain shadow effects are prominent, resulting in near-desert vegetation. The geology has a basin and range structure resulting primarily from the Late Tertiary uplift of the Central Andes.

The Andes Mountains decrease in elevation to ~2000 m south of the Juan Fernández Ridge (33°S). Subduction of this section of the Nazca Plate steepens, and there are volcanic highlands with intervening valleys (e.g., the Central Valley of Chile; Fig. 1.45). The Central Valley is flooded south of Puerto Montt (41°S) through subsidence and dragging down of the continental shelf by the descending Nazca Plate (Clapperton, 1993; Fig. 2.46).

The Southern Andes—This segment of the comparatively low Andes Mountains begins where the South America, Nazca, and Antarctic plates form a triple junction near 46°S (Fig. 2.37). There was collision and subduction of the Pacific Plate (Farallon-Aluk Ridge) in the Eocene, two intervals of rapid plate convergence at 50–42 Ma and 25–10 Ma (Suárez et al., 2000), and subduction of the Chile Ridge in the Miocene to Recent. The convergence of the plates uplifted the Taitao Peninsula off the Pacific coast of Patagonia, while much of the rest of the landscape originated as low mountainous Cretaceous island arcs accreted onto the mainland with a generally west to east development of the highlands. There are also some lava plateaus resulting from limited back-arc vol-

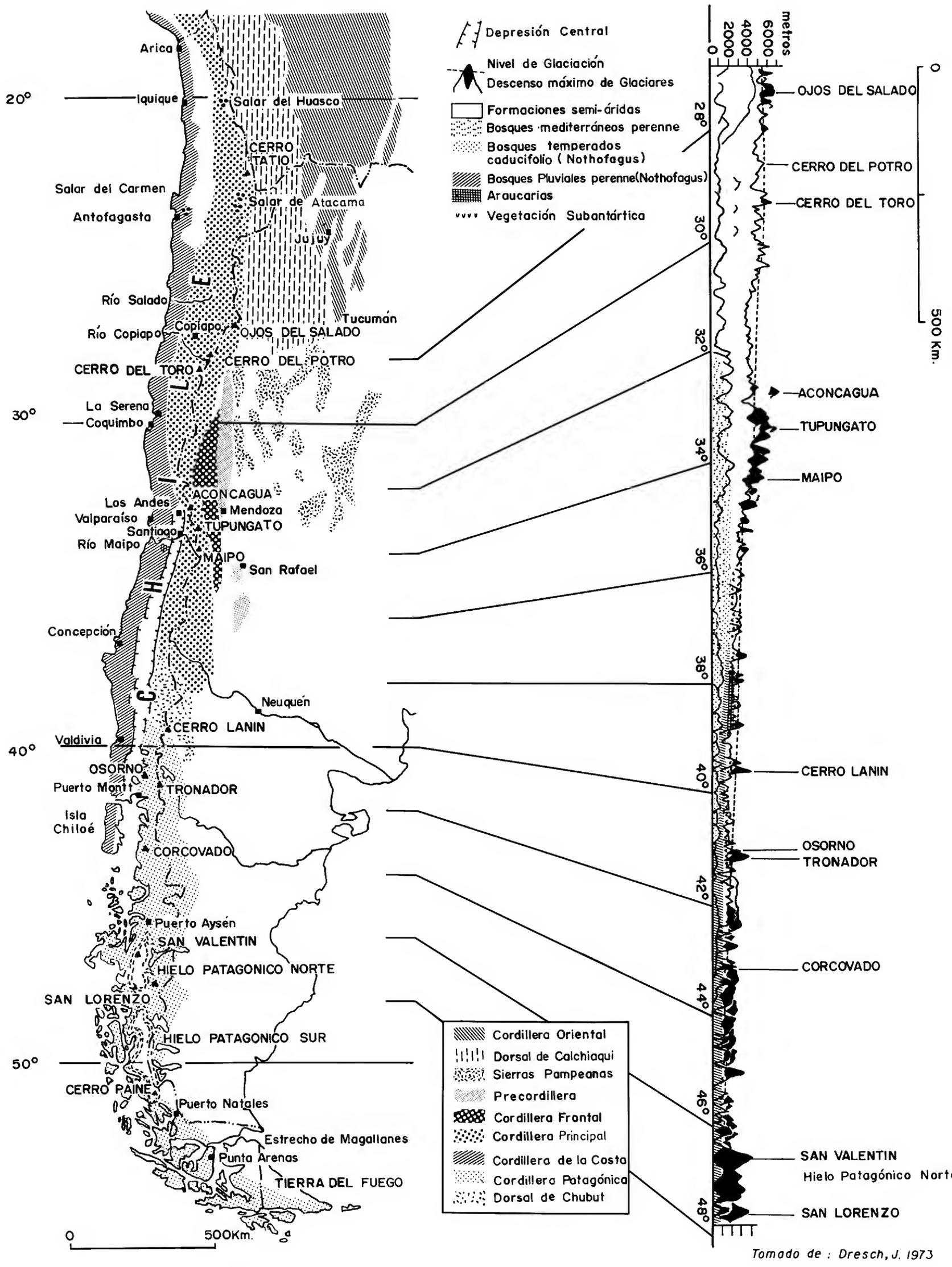


Figure 2.46. Geomorphic structures of the Andean Province of Chile. From Frutos (1986a). Used with permission of Editorial de la Universidad de Concepción, Concepción, Chile.

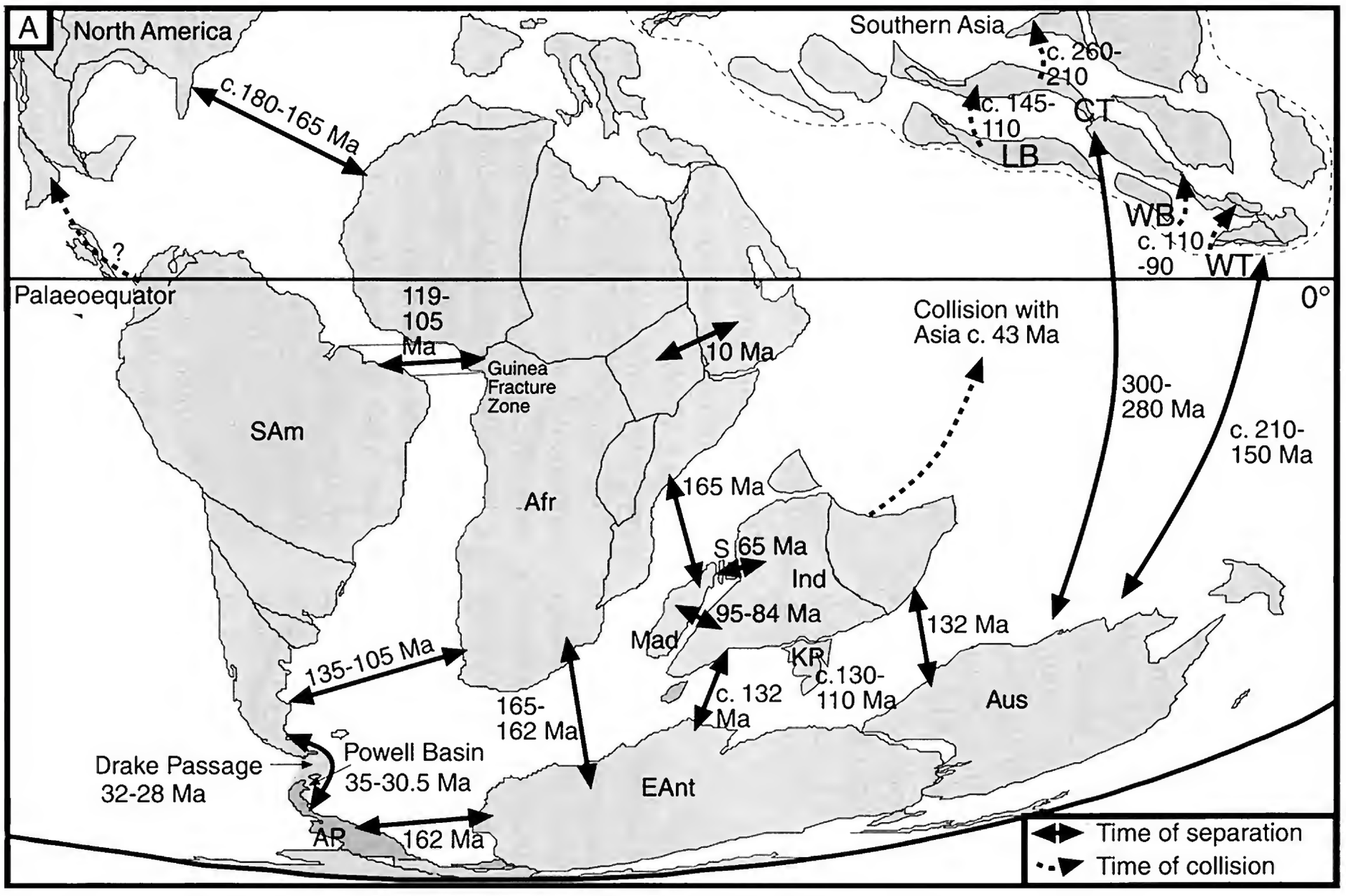


Figure 2.47. Breakup of Gondwana. From McLoughlin (2001). Used with permission from the *Australian Journal of Botany* 49(3): 271–300 (S. McLoughlin), CSIRO Publishing, Melbourne (http://www.publish.csiro.au/nid/66/issue/430.htm).

canism. The Andes Mountains terminate in Tierra del Fuego (~52°S), where convergence of the South America, Antarctic, and Scotia plates has uplifted the Cordillera Darwin to just over 2000 m. The earliest record of Cenozoic glaciation in South America is from Patagonia, where tills are present beneath basalts of Miocene to Quaternary age, and Mercer et al. (1975) note evidence of glaciation by 3.5 Ma. Glacial rivers have cut large basins into the landscape, such as Lago Buenos Aires in western Argentina, Sarmiento Basin in central Patagonia, and Lago Fagnano in the southern part of the Isla Grande de Tierra del Fuego. The Quaternary history of Tierra del Fuego is reviewed by Rabassa et al. (2000). In contrast to the rugged and majestic scenery of western Patagonia (Fig. 1.49), the eastern (Atlantic) side slopes to a glacial plain composed of outwash sands and gravel filling older pull-apart basins that were remnants of the separation of South America from Africa. These basins, lagoons, and intercalated ash deposits preserve a rich sequence of fossil floras and faunas in Patagonia (Chapter 7).

South America as an Island Continent

The breakup of Gondwana (Fig. 2.47; McLoughlin, 2001) began ~180 Ma (Jurassic) between southern Africa and South America, although some contact was possibly provided by the Falklands Plateau (MacPhail & Cantrill, 2006) until ~105 Ma (Barron, 1987). Full separation between Africa and South America dates from ~90 Ma.

Later, two other events occurred that are important to the biotic and climatic history of the region. One was the separation of South America from Antarctica. There is evidence of attenuation (thinning of strata) between South America and Antarctica from ~162–130 Ma with opening of the Rochas Verdes Basin in southern Chile. However, full separation of these continents was not achieved until the Oligocene between ~35 and 30.5 Ma with subsidence to form the Powell Basin, and 32 and 28 Ma with sea-floor spreading in the Scotia Sea to form the Drake Passage (see Fig. 8.27). This disrupted the previously continuous land from southern South America through West Antarctica to southern Australia—a physiographic-biotic province including Weddellia (Fig. 8.28). Australia separated from Antarctica ~49 Ma. The other event was structural separation and removal of any submerged sill impeding the formation of a circum-Antarctic current thermally isolating Antarctica from warmer waters. This was accomplished ~30 Ma and contributed to full continental glaciation, cooling of South Atlantic waters from global climatic trends augmented by glacial runoff, and formation of the Humboldt Current. With that event, South America became isolated as an island continent for ~30 Ma and it would not be connected to Central and North America until ~3.5–3.1 Ma.

Mountain Uplift–Climate Change–Mountain Uplift (Working It Both Ways)

It is generally recognized that when major mountain systems or plateaus rise, this causes a change in climate by altering atmospheric circulation, increasing erosion with a consequent drawdown of CO_2, deflecting precipitation, and creating wet (windward) and dry (leeward) habitats. Molnar and England (1990) proposed a model whereby climate may also facilitate mountain uplift through increased erosion with subsequent isostatic rebound of the land (see also Montgomery et al., 2001). Raymo and Ruddiman (1992, p. 122) and others have suggested a combined version:

> "It is consistent with both hypotheses to argue that uplift of Tibet (and possibly elsewhere) is a plausible first cause of Cenozoic climatic changes (through circulation changes and weathering), but that climatic change (in particular, glacier activity) then caused additional erosion, exhumation and isostatic uplift in other regions… . Thus, the arguments of Molnar and England can be viewed as a positive feedback mechanism, whereby uplift-induced erosion initiates global cooling, which then causes further glacial erosion and cooling worldwide." (I: p. 55)

This brief outline of the Late Cretaceous and Cenozoic geology of Latin America describes the general construction of the landscape in Late Cretaceous and Cenozoic times. It is essential context information for understanding biotic history because it reveals the environments, structures, events, processes, and the timing of factors that had impact on the assemblages living in the great basins, plains, and mountain systems of Latin America. The nature of the environment is revealed by swamp, lagoonal, fluvial, lacustrine, and glacial deposits and by the development of extensive alluvial fans, compared to the presence of red beds, evaporites (salt, gypsum), and aeolian deposits (loess, dunes). The development of geologic structures influences ecosystems as shown by fault-defined wetlands, as well as speciation and evolutionary patterns as shown by the residual effect of the Iquitos and other arches in the Amazon Basin. Geologic events and processes of climatic and biological importance include accretion of distant terranes onto mainlands; subduction, compression, subsidence, uplift, fragmentation of landmasses; rain shadows; volcanism; cycles of inundation and drainage (with concomitant isolation and uniting of populations); drainage reversals; lithosphere thinning; and the appearance of submarine fans and deltas. There is a wealth of biologically relevant information to be read from physical and historical geology, and it serves as a context for interpreting the fossil floras and faunas. Equally important is that it shows how landscapes and environments fluctuated over time, requiring a dynamic view of biotic history. Although this may seem self-evident from a modern perspective, tropical communities were depicted quite differently in much of the literature through the 1960s. They were supposed to have "extended uninterruptedly since a very remote geological period" and under "seasonal and geological stability of the climate" (see Chapter 8, Climate, Vegetation, and the Stability of Tropical Ecosystems). These are curious conclusions in light of the virtual absence at the time of any paleobotanical information about Late Cretaceous and Cenozoic vegetation in the tropics, and considering the suggestion by Humboldt (1807) that the Neotropical biota had probably undergone considerable change during the geologic past. A product of these changes is the modern version of the plant formations of Latin America discussed in Chapter 3, and which serve as the goal or end point of the histories presented in Chapters 4–7.

NOTES

1. In addition to gold discovered on Hispaniola by Columbus in 1493 and oil seepages found by Castellanos on Cubagua in 1589, natural plant resources were to have an equally profound social and economic impact throughout Latin America:

> "In 1714 the Dutch gave a healthy coffee plant to the French government, and nine years later an obsessed French naval officer, Gabriel Mathieu de Clieu, introduced coffee cultivation to the French colony of Martinique. After considerable court intrigue, he obtained one of the Dutch offspring plants from the Jardin des Plantes in Paris and nursed it during a perilous transatlantic voyage, later referring to 'the infinite care that I was obliged to bestowe upon this delicate plant.' After avoiding capture by a corsair and surviving a tempest, de Clieu's ship floundered in windless doldrums for over a month. The Frenchman protected his beloved plant from a jealous fellow passenger and shared his limited supply of water with it. Once it finally set down roots in Martinique, the coffee tree flourished. From that single plant much of the world's current coffee supply probably derives.
>
> Then, in 1727, a mini-drama led to the fateful introduction of coffee into Brazil. To resolve a border dispute, the governors of French and Dutch Guiana asked a neutral Portuguese Brazilian official named Francisco de Melho Palheta to adjudicate. He quickly agreed, hoping that he could somehow smuggle out coffee seeds, since neither governor would allow the seeds' export. The mediator successfully negotiated a compromise border solution and clandestinely bedded the French governor's wife. At Palheta's departure, she presented him with a bouquet of flowers with ripe coffee berries disguised in the interior. He planted them in his home territory of Pará, from which coffee gradually spread southward."

Prior to that intrigue, coffee had a turbulent time also in Europe. Women were excluded from the coffee houses in London, and in 1674 they issued *The Womens Petition Against Coffee*:

"We find of late a very sensible decay of that true Old English Vigour…Never did Men wear greater Breeches, or carry less in them of any *Mettle* whatsoever"… This condition was all due to "the Excessive use of that Newfangled, Abominable, Heathenish Liquor called Coffee, which…has so Eunucht our husbands, and *Crippled* our more kind *gallants*…They come from it with nothing moist but their snotty Noses, nothing stiffe but their Joints, nor standing but their Ears." (Mark Pendergrast, 1999, *Uncommon Grounds*, Basic Books, New York; see also Anthony Clayton, 2003, *London's Coffee Houses: A Stimulating Story*, Historical Publications, London.)

REFERENCES

Albert, J. S., N. R. Lovejoy, and W. G. R. Crampton. 2006. Miocene tectonism and the separation of cis- and trans-Andean river basins: Evidence from Neotropical fishes. J. S. Amer. Earth Sci. 21: 14–27.

Albertão, G. A. and P. P. Martins Jr. 1996. A possible tsunami deposit at the Cretaceous–Tertiary boundary in Pernambuco, northeastern Brazil. Sedimentary Geol. 104: 189–201.

Anderson, T. H. 1968. First evidence for glaciation in the Sierra de Los Cuchumatanes Range, northwestern Guatemala. Abstract, Geol. Soc. Amer. Spec. Paper 121: 387.

———, R. J. Erdlac, and M. A. Sandstrom. 1985. Late Cretaceous allochthons and post-Cretaceous strike-slip displacement along the Cuilco–Chixoy–Polochic fault, Guatemala. Tectonics 5: 453–475.

Aslan, A. et al. (+ 6 authors). 2001. Mud volcanoes of the Orinoco Delta, eastern Venezuela. Geomorphology 41: 323–336.

Babeyko, A. Y. and S. V. Sobolev. 2005. Quantifying different modes of the late Cenozoic shortening in the central Andes. Geology 33: 621–624.

Bader, R. G. et al. (+ 23 authors). 1970. Initial Reports of the Deep Sea Drilling Project, Vol. 4. U.S. Government Printing Office, Washington, D.C.

Barreda, V. D., S. Palamarczuk, and J. A. Chamberlain Jr. 2004. Vegetational disruption at the Cretaceous/Paleocene boundary in Neuquén, Argentina: Evidence from spores and pollen. Abstract, 10th Reunión Argentina Sedimentologia (San Luis, Argentina, 2004).

Barron, E. J. 1987. Cretaceous plate tectonic reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 59: 3–29.

Beard, J. S. 1949. The Natural Vegetation of the Windward and Leeward Islands. Clarendon Press, Oxford, U.K.

Bellizzia, A. and G. Dengo. 1990. The Caribbean mountain system, northern South America; a summary. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 167–175.

Bolay, E. 1997. The Dominican Republic: A Country between Rain Forest and Desert: Contributions to the Ecology of a Caribbean Island. Margraf, Weikersheim, Germany.

Bonaparte, J. F. 1984. El intercambio faunístico de vertebrados continentals entre América del Sur y del Norte a fines del Cretácico. Memoria 3rd Congresso Latinoamericano de Paleontología, Oaxtepec, México. pp. 438–450.

——— and J. E. Powell. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda–Coelurosauria–Carnosauria–Aves). Mém. Soc. Geol. France n.s. 139: 19–28.

Borhidi, A. 1996. Phytogeography and Vegetation Ecology of Cuba. Akadémiai Kiadó, Budapest.

Bottke, W. F., D. Vokrouhlicky, and D. Nesvorný. 2007. An asteroid breakup 160 Myr ago as the probable source of the K/T impactor. Nature 449: 48–53.

Breedlove, D. E. 1973. The phytogeography and vegetation of Chiapas (Mexico). *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 149–165.

———. 1981. Introduction to the flora of Chiapas. *In:* D. E. Breedlove (ed.), Flora of Chiapas, part 1. California Academy of Sciences, San Francisco. pp. 1–35.

Burkart, B. 1978. Offset across the Polochic fault of Guatemala and Chiapas, Mexico. Geology 6: 328–332.

———. 1983. Neogene North American–Caribbean plate boundary across northern Central America: Offset along the Polochic fault. Tectonophysics 99: 251–270.

——— and G. Moreno. 1983. North American–Caribbean plate boundary in southern Chiapas, Mexico: Further evidence of Neogene activity. Abstract, Programa 10th Conferencia Geológica del Caribe (Cartagena). p. 28.

——— and B. Self. 1985. Extension and rotation of crustal blocks in northern Central America and its effect upon the volcanic arc. Geology 13: 22–26.

Burke, K., C. Cooper, J. F. Dewey, P. Mann, and J. L. Pindell. 1984. Caribbean tectonics and relative plate motions. *In:* W. E. Bonini, R. B. Hargraves, and R. Shagam (eds.), The Caribbean–South American Plate Boundary and Regional Tectonics. Geol. Soc. Amer. Mem. 162: 31–63.

Buskirk, R. E. 1985. Zoogeographic patterns and tectonic history of Jamaica and the northern Caribbean. J. Biogeogr. 12: 445–461.

Butterlin, J. 1956. La Constitution Géologique et la Structure de Antilles. Centre Nationale de la Rechérche Scientifique, Paris.

———. 1960. Géologié Générale et Régionale de la Republique d'Haiti. Travaux et Memoires de l'Institut des Hautes Etudies de l'Amérique Latine, Universite de Paris, Paris.

Campbell, K. E., Jr., C. D. Frailey, and L. Romero-Pittman. 2006. The pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239: 166–219.

———, M. Heizler, C. D. Frailey, L. Romero-Pittman, and D. R. Prothero. 2001. Upper Cenozoic chronostratigraphy of the southwestern Amazon Basin. Geology 29: 595–598.

Campos-Enriquez, J. O., J. Ortega-Ramírez, D. Alatriste-Vilchis, R. Cruz-Gática, and E. Cabral-Cano. 1999. Relationship between extensional tectonic style and the paleoclimatic elements at Laguna El Fresnal, Chihuahua Desert, Mexico. Geomorphology 28: 75–94.

Case, J. E. and G. Dengo. 1990. Foreword. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. ix–x.

———, W. D. MacDonald, and P. J. Fox. 1990. Caribbean crustal provinces; seismic and gravity evidence. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 15–36.

Castillo-Muñoz, R. 1983. Geology. *In:* D. H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago. pp. 47–62.

———. 1984. Geología de Costa Rica, una Sinopsis. Editorial de la Universidad de Costa Rica, San Pedro.

Chazdon, R. L. and the Earl of Cranbrook. 2002. Tropical naturalists of the sixteenth through nineteenth centuries. *In:* R. L. Chazdon and T. C. Whitmore (eds.), Foundations of Tropical Forest Biology: Classic Papers with Commentaries. University of Chicago Press, Chicago. pp. 5–21.

Christie, D. M. et al. (+ 6 authors). 1992. Drowned islands downstream from the Galápagos hotspot imply extended speciation times. Nature 355: 246–248.

Clapperton, C. 1993. Quaternary Geology and Geomorphology of South America. Elsevier Science Publishers, Amsterdam.

Cleve, P. T. 1871. On the geology of the northeastern West India Islands. Svenska Vetenskapsakad. Handl. 12: 1–48.

Coates, A. G. (ed.). 1997. Central America: A Natural and Cultural History. Yale University Press, New Haven, CT.

——— et al. (+ 7 authors). 1992. Closure of the Isthmus of Panama: The near-shore marine record of Costa Rica and western Panama. Geol. Soc. Amer. Bull. 104: 814–828.

Collins, L. S. and A. G. Coates (eds.). 1999. A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama. Bull. Amer. Paleontol. 357: 5–351.

Coltorti, M. et al. (+ 5 authors). 1998. The last occurrence of Pleistocene megafauna in the Ecuadorian Andes. J. S. Amer. Earth Sci. 11: 581–586.

——— and C. D. Ollier. 2000. Geomorphologic and tectonic evolution of the Ecuadorian Andes. Geomorphology 32: 1–19.

Commission de la Carte Géologique du Monde. 1964. Carte Géologique de L'Amerique du Sud. Ministério das Minas e Energia, Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil. Escala 1:5,000,000.

Cooke, C. W., J. Gardner, and W. P. Woodring. 1943. Correlation of the Cenozoic formations of the Atlantic and Gulf coastal plain and the Caribbean region. Geol. Soc. Amer. Bull. 54: 1713–1723.

Corral, J. I. 1939. La unión de Cuba con el continente Americano. Revista Soc. Cub. Ing. 33: 582–681.

Cros, P., F. Michaud, E. Fourcade, and J. J. Fleury. 1998. Sedimentological evolution of the Cretaceous carbonate platform of Chiapas (Mexico). J. S. Amer. Earth Sci. 11: 311–332.

Dalton, R. 2007. Time traps. Nature 449: 20–21.

de Cserna, Z. 1989. An outline of the geology of Mexico. *In:* A. W. Bally and A. R. Palmer (eds.), The Geology of North America, Vol. A, An Overview. Geological Society of America, Boulder, CO. pp. 233–264.

———. 1990. La evolución de la geología en México (~1500–1929). Univ. Nac. Autón. Méx., Inst. Geol., Revista 9: 1–20.

de la Beche, H. T. 1827. Remarks on the geology of Jamaica. Geol. Soc. London Trans., Ser. 2, 2: 143–194. [Accompanying map dated 1823.]

DeMets, C., R. G. Gordon, D. F. Argus, and S. Stein. 1990. Current plate motions. Geophys. J. Int. 101: 425–478.

Dengo, G. 1969a. Problems of tectonic relations between Central America and the Caribbean. Trans. Gulf Coast Assoc. Geol. Soc. 29: 311–320.

———. 1969b. Mapa metalogenético de América Central. Publ. Geol. ICAITI. Scale 1:200,000. [See also Dengo, G. and E. Levy. 1970. Anotaciones al mapa metalogenético de América Central. Publ. Geol. ICAITI 3: 1–15; explanatory text.]

——— and O. H. Bohnenberger. 1969. Structural development of northern Central America. Amer. Assoc. Petrol. Geol. Mem. 11: 203–220.

Dixon, T. H., F. Farina, C. DeMets, P. Jansma, P. Mann, and E. Calais. 1998. Relative motion between the Caribbean and North American plates and related boundary zone of deformation from a decade of GPS observations. J. Geophys. Res. 103: 15,157–15,182.

Dollfus, A. and E. Montserrat. 1868. Voyage Géologique dans les Républiques de Guatemala et de Salvador. Mission Scientifique au Mexique et dans l'Amerique Central. Paris.

Donnelly, T. W. 1985. Mesozoic and Cenozoic plate evolution of the Caribbean region. *In:* F. G. Stehli and S. D. Webb (eds.), The Great American Biotic Interchange. Plenum Press, New York. pp. 89–121.

———. 1989a. Geologic history of the Caribbean and Central America. *In:* A. W. Bally and A. R. Palmer (eds.), The Geology of North America, Vol. A, An Overview. Geological Society of America, Boulder, CO. pp. 299–321.

———. 1989b. History of marine barriers and terrestrial connections: Caribbean paleogeographic inference from pelagic sediment analysis. *In:* C. A. Woods (ed.), Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, FL. pp. 103–118.

———. 1994. The Caribbean Cretaceous basalt association: A vast igneous province that includes the Nicoya Com-

plex of Costa Rica. *In:* H. Seyfried and W. Hellmann (eds.), Geology of an Evolving Island Arc: The Isthmus of Southern Nicaragua, Costa Rica, and Western Panamá. Profil (Institut für Geologie und Paläontologie, Universität Stuttgart) 7: 17–45.

———, G. S. Horne, R. C. Finch, and E. López-Ramos. 1990a. Northern Central America; the Maya and Chortis blocks. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 37–76.

——— et al. (+ 9 authors). 1990b. History and tectonic setting of Caribbean magmatism. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 339–374.

Dowsett, H. J. and T. M. Cronin. 1990. High eustatic sea level during the middle Pliocene: Evidence from the southeastern U.S. coastal plain. Geology 18: 435–438.

Draper, G. and J. A. Barros. 1994. Cuba. *In:* S. K. Donovan and T. A. Jackson (eds.), Caribbean Geology: An Introduction. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica. pp. 65–86.

——— and G. Dengo. 1990. History of geological investigation in the Caribbean region. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 1–14.

Drewes, H. 1978. The cordilleran orogenic belt between Nevada and Chihuahua. Geol. Soc. Amer. Bull. 89: 641–657.

Driscoll, N. W. and J. B. Diebold. 1999. Tectonic and stratigraphic development of the eastern Caribbean: New constraints from multichannel seismic data. *In:* P. Mann (ed.), Caribbean Basins. Elsevier Science Publishers, Amsterdam. pp. 591–626.

Drummond, M. S. et al. (+ 5 authors). 1995. Igneous petrogenesis and tectonic setting of plutonic and volcanic rocks of the Cordillera de Talamanca, Costa Rica–Panama Central American arc. Amer. J. Sci. 295: 875–919.

Duncan, R. A. and R. B. Hargraves. 1984. Plate tectonic evolution of the Caribbean region in the mantle reference frame. *In:* W. E. Bonini, R. B. Hargraves, and R. Shagam (eds.), The Caribbean–South American Plate Boundary and Regional Tectonics. Geol. Soc. Amer. Mem. 162: 81–93.

Dupuget. 1796. Extrait d'un memoire du citoyen Dupuget, intitulé: Coupe d'oeil rapide sur la physique generale et la mineralogie des Antilles. J. Mines 3: 43–60. [Published, cited, and databased without author initial(s).]

Emiliani, C. 1982. A new global geology. *In:* C. Emiliani (ed.), The Oceanic Lithosphere. John Wiley & Sons, New York. pp. 1687–1728.

Escalante, G. 1990. The geology of southern Central America and western Colombia. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 201–230.

Espinosa, A. F. (ed.). 1976. The Guatemalan Earthquake of February 4, 1976, a Preliminary Report. U.S. Geol. Surv. Prof. Paper 1002: 1–90.

———, R. Husid, and A. Quesada. 1976. Intensity distribution and source parameters from field observations. *In:* A. F. Espinosa (ed.), The Guatemalan Earthquake of February 4, 1976, a Preliminary Report. U.S. Geol. Surv. Prof. Paper 1002: 52–66.

Eva, A. N. and N. A. McFarlane. 1985. Tertiary to early Quaternary carbonate facies relationships in Jamaica. Trans. 4th Latin American Geological Conference, Port-of-Spain, Trinidad and Tobago (1979). pp. 210–219.

Fernandez de Castro, M. 1884. Pruebas paleontológicas de que la Isla de Cuba ha estado unida al continente Americano y breve idea de su constitutíon geológica. Anales Acad. Ci. Habana 21: 146–165.

Ferrusquía-Villafranca, I. 1993. Geology of Mexico: A synopsis. *In:* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa (eds.), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, Oxford, U.K. pp. 3–107.

———, L. I. González Guzmán, and J.-L. E. Cartron. 2005. Northern Mexico's landscape, part I: The physical setting and constraints on modeling biotic evolution. *In:* J.-L. Cartron, G. Ceballos, and R. S. Felger (eds.), Biodiversity, Ecosystems, and Conservation in Northern Mexico. Oxford University Press, Oxford, U.K. pp. 11–38.

Ficcarelli, G. et al. (+ 8 authors). 1997. Hypothesis on the cause of extinctions of the South American mastodonts. J. S. Amer. Earth Sci. 10: 29–38.

Ford, I., J. Montaña, and H. Morales. 1990. Carta Geológica del Uruguay, Hoja N-19, Paso del Palmar. Facultad de Agronomía, Montevideo, Uruguay. Escala 1:100,000. [See also H. Morales et al., 1990, Hoja 0–19, Cololó, et seq.]

Forsberg, B. R., Y. Hashimoto, Å. Rosenqvist, and F. Pellon de Miranda. 2000. Tectonic fault control of wetland distributions in the central Amazon revealed by JERS-1 radar imagery. Quatern. Int. 72: 61–66.

Foshag, W. F. and J. González R. 1956. Birth and development of Parícutin volcano. U.S. Geol. Surv. Bull. 965-D: 355–489.

Freeland, G. L. and R. S. Dietz. 1971. Plate tectonic evolution of the Caribbean–Gulf of Mexico region. Nature 232: 20–23.

Fries, C., Jr. 1960. Geología del estado de Morelos y de partes adyacentes de México y Guerrero, región central meridional de México. Inst. Geol., UNAM, Bol. 60: 1–236.

Frost, S. H. and R. L. Langenheim Jr. 1974. Cenozoic Reef Biofacies, Tertiary Larger Foraminifera and Scleractinian Corals from Chiapas, Mexico. Northern Illinois University Press, De Kalb, IL.

Frutos, J. 1986a. La Cordillera de Los Andes: Palabras de presentación. *In:* J. Frutos, R. Oyarzúm, and M. Pincheira (eds.), Geología y Recursos Minerales de Chile. Editorial de la Universidad de Concepción, Concepción, Chile. pp.

5–9.

———. 1986b. La Cordillera de Los Andes: Características geofísicas, estructura y dinámica del margen continental Andio. *In:* J. Frutos, R. Oyarzúm, and M. Pincheira (eds.), Geología y Recursos Minerales de Chile. Editorial de la Universidad de Concepción, Concepción, Chile. pp. 29–62.

———, R. Oyazúm, and M. Pincheira (eds.). 1986. Geología y Recursos Minerales de Chile. Editorial de la Universidad de Concepción, Concepción, Chile.

Gabb, W. M. 1873. Topography and geology of Santo Domingo. Trans. Amer. Philos. Soc., n.s., 15: 49–259.

———. 1874a. Note on the geology of Costa Rica. Amer. J. Sci. 7: 438–439.

———. 1874b. Notes on the geology of Costa Rica. Amer. J. Sci. 8: 388–390.

———. 1875. Notes on the geology of Costa Rica. Amer. J. Sci. 9: 198–204.

Gansser, A. 1973. Facts and theories on the Andes. J. Geol. Soc. 129: 93–131.

Ghosh, P., C. N. Garzione, and J. M. Eiler. 2006. Rapid uplift of the Altiplano revealed through ^{13}C–^{18}O bonds in paleosol carbonates. Science 311: 511–515. [See also Technical Comment Abstracts, Science 314: 760.]

Gibbs, A. K. and C. N. Barron. 1993. The Geology of the Guiana Shield. Oxford Monographs on Geology and Geophysics. Oxford University Press, Oxford, U.K.

Giles, J. 2005. Geologists call time on dating dispute. Nature 435: 865.

Gingerich, P. D. 1985. South American mammals in the Paleocene of North America. *In:* F. G. Stehli and S. D. Webb (eds.), The Great American Biotic Interchange. Plenum Press, New York. pp. 123–137.

Gordon, M. B., P. Mann, D. Cáceres, and R. Flores. 1997. Cenozoic tectonic history of the North America–Caribbean plate boundary in western Cuba. J. Geophys. Res. 102: 10,055–10,082.

Graham, A. 2003. Historical phytogeography of the Greater Antilles. Brittonia 55: 357–383.

Guilderson, T. P., R. G. Fairbanks, and J. L. Rubenstone. 1994. Tropical temperature variations since 20,000 years ago: Modulating interhemispheric climate change. Science 263: 663–665.

Guzmán-Speziale, M. and J. J. Meneses-Rocha. 2000. The North American–Caribbean plate boundary west of the Motagua-Polochic fault system: A fault jog in southeastern Mexico. J. S. Amer. Earth Sci. 13: 459–468.

Haq, B. L., J. Hardenbol, and P. R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235: 1156–1167.

Hartley, A. J. 2003. Andean uplift and climate change. J. Geol. Soc. London 160: 7–10.

Hastenrath, S. 1973. On the Pleistocene glaciation of the Cordillera de Talamanca, Costa Rica. Z. Gletscherkunde Glaziageologie 9: 105–121.

Hauff, F., K. Hoernle, H.-U. Schmincke, and R. Werner. 1997. A Mid Cretaceous origin for the Galápagos hotspot: Volcanological, petrological and geochemical evidence from Costa Rican oceanic crustal segments. Geol. Rundschau. 86: 141–155.

Hedges, S. B. 2006. Paleogeography of the Antilles and origin of West Indies terrestrial vertebrates. *In:* A. Graham (ed.), Latin American Biogeography—Causes and Effects. Ann. Missouri Bot. Gard. 93: 231–244.

Hess, H. H. and J. C. Maxwell. 1953. Caribbean research project. Geol. Soc. Amer. Bull. 64: 1–6.

Hildebrand, A. R., M. Pilkington, M. Connors, C. Ortiz-Aleman, and R. E. Chavez. 1995. Size and structure of the Chicxulub crater revealed by horizontal gravity gradients and cenotes. Nature 376: 415–417.

Hill, R. T. 1894 et seq. Notes on the Tertiary and later history of Cuba. Amer. J. Sci. 48: 196–212.

Holcombe, T. L., J. W. Ladd, G. Westbrook, N. T. Edgar, and C. L. Bowland. 1990. Caribbean marine geology; ridges and basins of the plate interior. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 231–260.

Hooghiemstra, H. and E. T. H. Ran. 1994. Late Pliocene–Pleistocene high resolution pollen sequence of Colombia: An overview of climatic change. Quatern. Int. 21: 63–80.

Hoorn, C. 1994a. Fluvial palaeoenvironments in the intracratonic Amazonas Basin (early Miocene–early middle Miocene, Colombia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 1–54.

———. 1994b. An environmental reconstruction of the palaeo–Amazon River system (middle–late Miocene, NW Amazonia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 112: 187–238.

———, J. Guerrero, G. A. Sarmiento, and M. A. Lorente. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene South America. Geology 23: 237–240.

Horn, S. P. and K. A. Haberyan. 1993. Costa Rican lakes: Physical and chemical properties. Res. & Explor. 9: 86–103.

Horton, B. K., B. A. Hampton, and G. L. Waanders. 2001. Paleogene synorogenic sedimentation in the Altiplano Plateau and implications for initial mountain building in the Central Andes. Geol. Soc. Amer. Bull. 113: 1387–1400.

Huber, O. (ed.). 1992. El Macizo del Chimantá, Escudo de Guayana, Venezuela, un Ensayo Ecológico Tepuyana. Oscar Todtmann Editores, Caracas, Venezuela.

———. 1995. Geographic and physical features. *In*: J. A. Steyermark, P. E. Berry, and B. K. Holst (gen. eds.), Flora of the Venezuelan Guayana, Vol. 1. Missouri Botanical Garden, St. Louis, and Timber Press, Portland, OR. p. 5.

Humboldt, A. von. 1807. Essai sur la Géographie des Plantes. Levrault Schoell, Paris. [Reprinted 1977, Arno Press, New York.]

———. 1852. Personal narrative of travels to the equinoctal regions of the Americas (English translation and edition

by Thomasina Ross). Routledge, London. (Reprinted 1971, Blom, New York).

Hungerbühler, D. et al. (+ 7 authors). 2002. Neogene stratigraphy and Andean geodynamics of southern Ecuador. Earth Sci. Rev. 57: 75–124.

Iriondo, M. H. 1993. Geomorphology and late Quaternary of the chaco (South America). Geomorphology 7: 289–303.

———. 1999. The Neogene of the Llanos–Chaco–Pampa Depression. Episodes Int. Geosci. Newsmagazine 22: 226–231.

Israde-Alcantara, I. and V. H. Garduño-Monroy. 1999. Lacustrine record in a volcanic intra-arc setting: The evolution of the Late Neogene Cuitzeo basin system (central-western Mexico, Michoacán). Palaeogeogr. Palaeoclimatol. Palaeoecol. 151: 209–227.

Iturralde-Vinent, M. A. 1969. Principal characteristics of the Cuban Neogene stratigraphy. Bull. Amer. Assoc. Petrol. Geol. 53: 1938–1955.

———. 1978. Los movimientos tectónicos de la etapa de desarrollo platafórmico en Cuba. Geol. & Mijnb. 57: 205–212.

———. 1994. Cuban geology: A new plate tectonic synthesis. J. Petrol. Geol. 17: 39–70.

——— and L. Gahagan. 2002. Late Eocene to middle Miocene tectonic evolution of the Caribbean: Some principles and their implications for plate tectonic modeling. *In:* T. A. Jackson (ed.), Caribbean Geology into the Third Millennium. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica. pp. 47–62.

——— and R. D. E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science 273: 1850–1852.

——— and ———. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. Bull. Amer. Mus. Nat. Hist. 238: 1–95.

Jackson, T. A. (ed.). 2002. Caribbean Geology into the Third Millennium. Transactions of the Fifteenth Caribbean Geological Conference. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica.

Jukes-Brown, A. J. and J. B. Harrison. 1891. The geology of Barbados; Part I, The coral rocks of Barbados and other West Indian islands. Geol. Soc. London Quart. J. 47: 197–243.

——— and ———. 1892. The geology of Barbados; Part II, The oceanic deposits. Geol. Soc. London Quart. J. 48: 170–226.

Keigwin, L. D., Jr. 1982. Isotopic paleoceanography of the Caribbean and east Pacific: Role of Panama uplift in late Neogene time. Science 217: 350–353.

Kellum, L. B. 1944. Geologic history of northern Mexico and its bearing on petroleum exploration. Bull. Amer. Assoc. Petrol. Geol. 28: 301–325.

Kennan, L., S. Lamb, and C. Rundle. 1995. K-Ar dates from the Altiplano and Cordillera Oriental of Bolivia: Implications for Cenozoic stratigraphy and tectonics. J. S. Amer. Earth Sci. 8: 163–186.

Kesler, S. E., N. Russell, J. Polanco, K. McCurdy, and G. L. Cumming. 1991. Geology and geochemistry of the Early Cretaceous Los Ranchos Formation, central Dominican Republic. *In:* P. Mann, G. Draper, and J. F. Lewis (eds.), Geologic and Tectonic Development of the North America–Caribbean Plate Boundary in Hispaniola. Geol. Soc. Amer. Spec. Paper 262: 187–201.

Klammer, G. 1976. Zur jungquatären Reliefgeschichte des Amazonas-Tales. Geomorphol. N.F. (Berlin) 20: 149–170.

———. 1984. The relief of the extra-Andean Amazon Basin. *In:* H. Sioli (ed.), The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 47–83.

Krajick, K. 2002. Ice man: Lonnie Thompson scales the peaks for science. Science 298: 518–522.

Ladd, J. W., T. L. Holcombe, G. K. Westbrook, and N. T. Edgar. 1990. Caribbean geology; active margins of the plate boundary *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 261–290.

Lamb, S. 2004. Devil in the Mountain: A Search for the Origin of the Andes. Princeton University Press, Princeton, NJ.

——— and P. Davis. 2003. Cenozoic climate change as a possible cause for the rise of the Andes. Nature 425: 792–797.

Lehmann, C. et al. (+ 5 authors). 1999. Evolution of Cupido and Coahuila carbonate platforms, Early Cretaceous, northeastern Mexico. Geol. Soc. Amer. Bull. 111: 1010–1029.

Lewis, J. F. and G. Draper. 1990. Geology and tectonic evolution of the northern Caribbean margin. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 77–140.

Lovejoy, N. R., J. S. Albert, and W. G. R. Crampton. 2006. Miocene marine incursions and marine/freshwater transitions: Evidence from neotropical fishes. J. S. Amer. Earth Sci. 21: 5–13.

———, E. Bermingham, and A. P. Martin. 1998. Marine incursion into South America. Nature 396: 421–422.

Luhr, J. F., S. A. Nelson, J. F. Allan, and I. S. E. Carmichael. 1985. Active rifting in southwestern Mexico: Manifestations of an incipient eastward spreading-ridge jump. Geology 13: 54–57.

MacDonald, R., C. J. Hawkesworth, and E. Heath. 2000. The Lesser Antilles volcanic chain: A study in arc magmatism. Earth Sci. Rev. 49: 1–76.

MacPhail, M. and D. J. Cantrill. 2006. Age and implications of the Forest Bed, Falkland Islands, southwest Atlantic Ocean: Evidence from fossil pollen and spores. Palaeogeogr. Palaeoclimatol. Palaeoecol. 240: 602–629.

Malfait, B. T. and M. G. Dinkelman. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. Geol. Soc. Amer. Bull. 83: 251–272. [See also discussion by Meyerhoff and Meyerhoff, and reply,

84: 1105–1108.]

Malumián, N. 1999. La sedimentación y el volcanismo Terciarios en la Patagonia extraandina. I. La sedimentación en la Patagonia extraandina. Anales Inst. Geol. y Recursos Minerales Geol. Argent. 29: 577–612.

Mann, P. (ed.). 1999. Sedimentary Basins of the World, 4, Caribbean Basins. Elsevier Science Publishers, Amsterdam.

———, A. Escalona, and M V. Castillo. 2006. Regional geologic and tectonic setting of the Maracaibo supergiant basin, western Venezuela. Bull. Amer. Assoc. Petrol. Geol. 90: 445–477.

Mapa Geológico de Cuba. 1990. Academia Ciéncias de Cuba. Escala 1:250,000.

Marsh, S. P., D. H. Richter, S. Ludington, E. Soŕia-Escalante, and A. Escobar-Diaz. 1995. Digital Geologic Map of the Altiplano and Cordillera Occidental, Bolivia. U.S. Geol. Surv. Open-file Report 95–0494.

Martínez-Hernández, E., M. Sanchez López, and H. Hernández Campos. 1980. Palinología del Eoceno en el noreste de México. Abstract, IV Coloq. Paleobotánica Palinología (México D.F., 1980). pp. 25–26.

Maurrasse, F. J-M. R. 1982. Survey of the Geology of Haiti: Guide to the Field Excursions in Haiti. Miami Geological Society, Miami.

Maury, R. C., G. K. Westbrook, P. E. Baker, Ph. Bouysse, and D. Westcamp. 1990. Geology of the Lesser Antilles. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 141–166.

McLoughlin, S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Austral. J. Bot. 49(3): 271–300.

McNeill, D. F., A. G. Coates, A. F. Budd, and P. F. Borne. 2000. Integrated paleontologic and paleomagnetic stratigraphy of the upper Neogene deposits around Limón, Costa Rica: A coastal emergence record of the Central American Isthmus. Geol. Soc. Amer. Bull. 112: 963–981.

Mercer, J. H., R. J. Fleck, E. A. Mankinen, and W. Sander. 1975. Southern Patagonia: Glacial events between 4 m.y. and 1 m.y ago. *In:* R. P. Suggate and M. M. Cresswell (eds.), Quaternary Studies. Royal Society of New Zealand, Wellington. pp. 223–230.

Meschede, M. 1998. The impossible Galápagos connection: Geometric constraints for a near-American origin for the Caribbean plate. Geol. Rundschau. 87: 200–205.

———, U. Barckhausen, and H.-U. Worm. 2002. The evolution of the Cocos-Nazca spreading centre and overprinting hotspot traces. *In:* T. A. Jackson (ed.), Caribbean Geology into the Third Millennium. Transactions of the Fifteenth Caribbean Geological Conference. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica. pp. 63–72.

——— and W. Frisch. 1998. A plate-tectonic model for the Mesozoic and early Cenozoic history of the Caribbean plate. Tectonophysics 296: 269–291.

——— and ———. 2002. The evolution of the Caribbean plate and its relation to global plate motion vectors: Geometric constraints for an inter-American origin. *In:* T. A. Jackson (ed.), Caribbean Geology into the Third Millennium. Transactions of the Fifteenth Caribbean Geological Conference. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica. pp. 1–14.

Meyerhoff, A. A. and H. A. Meyerhoff. 1972. Continental drift, IV: The Caribbean "plate." J. Geol. 80: 34–60.

Minster, J.-B. and T. H. Jordon. 1978. Present-day plate motions. J. Geophys. Res. 83: 5331–5354.

Modenesi-Gauttieri, M. C., S. Takashi Hiruma, and C. Riccomini. 2002. Morphotectonics of a high plateau on the northwestern flank of the continental rift of southeastern Brazil. Geomorphology 43: 257–271.

Molnar, P. and P. England. 1990. Late Cenozoic uplift of mountain ranges and global climate change: Chicken or egg? Nature 346: 29–34.

Montgomery, D. R., G. Balco, and S. D. Willett. 2001. Climate, tectonics, and the morphology of the Andes. Geology 29: 579–582.

Mooser, F. 1975. Historia geológica de la cuenca de México. *In:* Mem. Obras Sistema Drenaje Profundo, Secretaría Obras Servicios Dept., I: 7–38. México, D.F.

Morán-Zenteno, D. J. et al. (+9 authors). 1999. Tertiary arc-magmatism of the Sierra Madre del Sur, Mexico, and its transition to the volcanic activity of the Trans-Mexican Volcanic Belt. J. S. Amer. Earth Sci. 12: 513–535.

Morris, A. E. L., I. Taner, H. A. Meyerhoff, and A. A. Meyerhoff. 1990. Tectonic evolution of the Caribbean region; alternative hypothesis. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 433–457.

Mpodozis, C. et al. (+ 5 authors). 2005. Late Mesozoic to Paleogene stratigraphy of the Salar de Atacama Basin, Antofagasta, northern Chile: Implications for the tectonic evolution of the Central Andes. Tectonophysics 399: 125–154.

Nieto-Samaniego, A. F., L. Ferrari, S. A. Alaniz-Alvarez, and G. Labarthe-Hernández. 1999. Variation of Cenozoic extension and volcanism across the southern Sierra Madre Occidental volcanic province, Mexico. Geol. Soc. Amer. Bull. 111: 347–363.

Nixon, G. T. 1982. The relationship between Quaternary volcanism in central Mexico and the seismicity and structure of subducted ocean lithosphere. Geol. Soc. Amer. Bull. 93: 514–523.

———. 1989. The geology of Iztaccíhuatl Volcano and adjacent areas of the Sierra Nevada and Valley of Mexico. Geol. Soc. Amer. Spec. Paper 219: 1–58.

Nuñez Molina, L. N. 1980. El Territorio Dominicano. Santo Domingo, Dominican Republic.

Ortega-Gutiérrez, F. et al. (+ 6 authors). 1992. Texto explicativo de la Quinta edición de la carta geológica de la República

Mexicana. Escala 1:2,000,000. Instituto de Geología, Instituto Geofísica, Universidad Nacional Autónoma de México, México, D.F.

Ortlieb, L. et al. (+ 5 authors). 1996. Coastal deformation and sea-level changes in the northern Chile subduction area (23°S) during the last 330 KY. Quatern. Sci. Rev. 15: 819–831.

Orvis, K. H., G. M. Clark, S. P. Horn, and L. M. Kennedy. 1997. Geomorphic traces of Quaternary climates in the Cordillera Central, Dominican Republic. Mountain Res. Develop. 17: 323–331.

———, S. P. Horn, and G. M. Clark. 2002. The case for late Pleistocene glaciers on Hispaniola. Abstract, Association of American Geographers (Los Angeles, CA, 2002).

Palacios, D. 1996. Recent geomorphic evolution of a glaciovolcanic active stratovolcano: Popocatépetl (Mexico). Geomorphology 16: 319–335.

Pascual, R. 1984. La sucesión de las edades-mamífero, de los climas y del diastrofismo Sudamericanos durante el Cenozoico: Fenómenos concurrentes. Anales Acad. Nac. Ci. Exact. Buenos Aires 36: 15–37.

———, M. Bond, and M. G. Vucetich. 1981. Subgrupo Santa Bárbara (Grupo Salta) y sus vertebrados. Cronología, paleoambientes y paleobiogeografía. Actas 8th Cong. Geol. Argentino (San Luis) 3: 743–758.

Pérez-Segura, E. and C. Jacques-Ayala (eds.). 1991. Studies of Sonoran Geology. Geol. Soc. Amer. Spec. Paper 254: 1–6.

Perfit, M. R. and E. E. Williams. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. *In:* C. A. Woods (ed.), Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, FL. pp. 47–102.

Pindell, J. L. 1994. Evolution of the Gulf of Mexico and the Caribbean. *In:* S. K. Donovan and T. A. Jackson (eds.), Caribbean Geology, An Introduction. The University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica. pp. 13–39.

——— and S. F. Barrett. 1990. Geological evolution of the Caribbean region; a plate-tectonic perspective. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America, Vol. H, The Caribbean Region. Geological Society of America, Boulder, CO. pp. 405–432.

——— et al. (+ 6 authors). 1988. A plate-kinematic framework for models of Caribbean evolution. Tectonophysics 155: 121–138.

Plafker, G., M. G. Bonilla, and S. B. Bonis. 1976. The Guatemala earthquake of February 4, 1976, a preliminary report, geologic effects. U.S. Geol. Surv. Prof. Paper 1002: 38–51.

Poinar, G., Jr. and R. Poinar. 1999. The Amber Forest: A Reconstruction of a Vanished World. Princeton University Press, Princeton, NJ.

Potter, P. E. 1997. The Mesozoic and Cenozoic paleodrainage of South America: A natural history. J. S. Amer. Earth Sci. 10: 331–344.

Preciozzi, F., J. Spoturno, W. Heinzen, and P. Rossi. 1980. Carta Geológica, 2da ed. Direción Nacional de Mineria y Geologia, Ministerio de Industria y Energia. Montevideo, Uruguay. Escala 1:500,000.

Putzer, H. 1984. The geological evolution of the Amazon Basin and its mineral resources. *In:* H. Sioli (ed.), The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin. Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 15–46.

Quattrocchio, M. E. and W. Volkheimer. 1990. Paleogene paleoenvironmental trends as reflected by palynological assemblage types, Salta Basin, NW Argentina. Neues Jahr. Geol. Paläont. Abh. 181: 377–396.

Rabassa, J. et al. (+ 10 authors). 2000. Quaternary of Tierra del Fuego, southernmost South America: An updated review. Quatern. Int. 68–71: 217–240.

Ramos, V. A. 1999. Plate tectonic setting of the Andean Cordillera. Episodes Int. Geosci. Newsmagazine 22: 183–190.

Räsänen, M. E., A. M. Linna, J. C. R. Santos, and F. R. Negri. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. Science 269: 386–390.

Raymo, M. E. and W. F. Ruddiman. 1992. Tectonic forcing of late Cenozoic climate. Nature 359: 117–122.

Rodríguez-Elizarrarás, S. R. 1995a. Estratigrafía y estructura del Volcán de Colima, México. Rev. Méx. Cien. Geol. 12: 22–46.

———. 1995b. Consideraciones preliminares sobre riesgo en el Volcán de Colima. Rev. Méx. Cien. Geol. 12: 47–51.

Ross, M. I. and C. R. Scotese. 1989. A hierarchial tectonic model of the Gulf of Mexico and Caribbean region. *In:* C. R. Scotese and W. W. Sager (eds.), Mesozoic and Cenozoic Plate Reconstructions. Elsevier Science Publishers, Amsterdam.

Ruiz Martínez, M. A. and J. Werner. 1997. Research into the Quaternary sediments and climatic variations in NE Mexico. Quatern. Int. 43/44: 145–151.

Russell, N. and S. E. Kesler. 1991. Geology of the Maar-Diatreme complex hosting precious metal mineralization at Pueblo Viejo, Dominican Republic. *In:* P. Mann, G. Draper, and F. F. Lewis (eds.), Geologic and Tectonic Development of the North America–Caribbean Plate Boundary in Hispaniola. Geol. Soc. Amer. Spec. Publ. 262: 203–215.

Sáez, A., L. Cabrera, A. Jensen, and G. Chong. 1999. Late Neogene lacustrine record and palaeogeography in the Quillagua–Llamara Basin, central Andean fore-arc (northern Chile). Palaeogeogr. Palaeoclimatol. Palaeoecol. 151: 5–37.

Salfity, J. A. and R. A. Marquillas. 1994. Tectonic and sedimentary evolution of the Cretaceous–Eocene Salta Group Basin, Argentina. *In:* J. A. Salfity (ed.), Cretaceous Tectonics of the Andes. Earth Evolution Sciences Monograph Series. Friedr. Vieweg & Sohn, Braunschweig/Wiesbaden, Germany. pp. 266–315.

Sauer, J. 1965. Geología del Ecuador. Ministerio de Educación,

Quito, Ecuador. [German translation, Geologie von Ecuador, 1971, Gerbrüder Borntraeger, Berlin.]
Sawkins, J. G. 1869. Reports on the Geology of Jamaica, with Contributions from G. P. Wall, L. Barrett, A. Lennox, and C. B. Brown. Longmans, London.
Schobbenhaus, C., D. de Almeida Campos, G. R. Derze, and H. E. Asmus (Coordenadores). 1984. Geología do Brasil. Texto Explicativa do Mapa Geológico do Brasil e da Área Oceânica Adjacente Incluindo Depósitos Minerais. Departamento Nacional da Produção Mineral. Brasília, Brasil. Escala 1:2,500,000.
Schubert, C. and E. Medina. 1982. Evidence of Quaternary glaciation in the Dominican Republic: Some implications for Caribbean paleoclimatology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 39: 281–294.
Schuchert, C. 1935. Historical Geology of the Antillean–Caribbean Region. Facsimile edition 1968, Hafner, New York.
Seebach, K. von. 1892. Über Vulkane Zentralamerikas. Dieterische Verlags-Buchhandlung, Göttingen, Germany.
Sempere, T. et al. (+ 5 authors). 1997. Stratigraphy and chronology of Upper Cretaceous–lower Paleogene strata in Bolivia and northwest Argentina. Geol. Soc. Amer. Bull. 109: 709–727.
Servicio Geológico de Bolivia. 1968. Mapa Geológico de la República de Bolivia. Servicio Geológico de Bolivia, La Paz. Escala 1:2,500,000.
Sheldon, N. D. 2005. Do red beds indicate paleoclimatic conditions? A Permian case study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 228: 305–319. ["…red color in general does not indicate specific paleoclimatic conditions."]
Singer, B. S. et al. (+ 9 authors). 1997. Volcanism and erosion during the past 930 k.y. at the Tatara-San Pedro complex, Chilean Andes. Geol. Soc. Amer. Bull. 109: 117–142.
Singh, S. K. et al. (+ 5 authors). 1980. The Oaxaca, Mexico earthquake of 29 November 1978: A preliminary report on aftershocks. Science 207: 1211–1213.
Sinton, C. W., R. A. Duncan, and P. Denyer. 1997. Nicoya Peninsula, Costa Rica: A single suite of Caribbean oceanic plateau magmas. J. Geophys. Res. 102 (B7): 15,507–15,520.
Smiley, C. J. 2002. Lower Cretaceous plants from the Dominican Republic. *In:* T. A. Jackson (ed.), Caribbean Geology into the Third Millennium. Transactions of the Fifteenth Caribbean Geological Conference. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica. pp. 119–130.
Smith, A. G., D. G. Smith, and B. M. Funnell. 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge, U.K.
Sobolev, S. V. and A. Y. Babeyko. 2005. What drives orogeny in the Andes? Geology 33: 617–620.
Speed, R. C. 1985. Cenozoic collision of the Lesser Antilles arc and continental South America and the origin of the El Pilar fault. Tectonics 4: 41–69.
——— and C. A. Keller. 1993. Synopsis of the geological evolution of Barbados. J. Barbados Mus. Hist. Soc. 41: 113–139.
———, P. L. Smith-Horowitz, K. v. S. Perch-Nielsen, J. B. Saunders, and A. B. Sanfilippo. 1993. Southern Lesser Antilles arc platform: Pre-late Miocene stratigraphy, structure, and tectonic evolution. Geol. Soc. Amer. Spec. Paper 277: 1–98.
Stewart, R. H. and J. L. Stewart (with the collaboration of W. P. Woodring). 1980. Geologic Map of the Panama Canal and Vicinity, Republic of Panama. Scale 1:1,000,000. U.S. Geological Survey Misc. Invest. Map I-1232. [Map also included in Woodring, 1982, U.S. Geol. Surv. Prof. Paper 306-F.]
Steyermark, J. A., P. E. Berry, and B. K. Holst. 1995. Flora of the Venezuelan Guayana, Vol. 2. Missouri Botanical Garden, St. Louis, and Timber Press, Portland, OR.
Suárez, M., R. de la Cruz, and C. M. Bell. 2000. Timing and origin of deformation along the Patagonian fold and thrust belt. Geol. Mag. 137: 345–353.
Taber, S. 1922. The great fault troughs of the Antilles. J. Geol. 30: 89–114.
Taylor, G. D. 1975. The geology of the Limón area of Costa Rica. Ph.D. dissertation, Louisiana State University, Baton Rouge.
Tilling, R. I. et al. (+ 5 authors). 1984. Holocene eruptive activity of El Chichón Volcano, Chiapas, Mexico. Science 224: 747–749.
U.S. Geological Survey and Corporación Venezolana de Guayana, Tecnica Minera, C.A. 1993. Geology and Mineral Resource Assessment of the Venezuelan Guayana Shield. U.S. Geol. Surv. Bull. 2062: 1–121.
U.S. Geological Survey Central Energy Team. 1999. South America Geologic Map (geo6 b and geo6 b.shp). U.S. Geological Survey Open File Report 97–4700.
U.S. Geological Survey–Servicio Geológico de Bolivia. 1992. Geology and mineral resources of the Altiplano and Cordillera Occidental, Bolivia. U.S. Geol. Surv. Bull. 1975: 1–365. [With accompanying geologic map, scale 1:500,000.]
Vajda, V. and S. McLoughlin. 2007. Extinction and recovery patterns of the vegetation across the Cretaceous–Palaeogene boundary—a tool for unraveling the causes of the end-Permian mass-extinction. Rev. Palaeobot. Palynol. 144: 99–112.
———, J. I. Raine, and C. J. Hollis. 2001. Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. Science 294: 1700–1702.
Vandel, A. 1973. Les isopods terrestres et cavernicoles del'Ile de Cuba. *In:* T. Orghidan et al. (eds.), Résultas des Expéditions Biospéleologiques Cubano-Roumaines à Cuba, Vol. 1. Editorial Academiei Republicii Socialiste Romania, Bucharest.
van der Hammen, T. 1952. Geología del Río Apaporis entre Soratama y Cachivera La Playa. Informe Servicio Geológica Nacional, Bogotá, Colombia: 834. [See also Rev. Territ. Nales. 4: 10–12, 1954.]
Vaughan, T. W. 1918. Geological history of Central America

and the West Indies during Cenozoic time. Geol. Soc. Amer. Bull. 29: 615–630.
Villamil, T. 1999. Campanian–Miocene tectonostratigraphy, depocenter, evolution and basin development of Colombia and western Venezuela. Palaeogeogr. Palaeoclimatol. Palaeoecol. 153: 239–275.
Vital, H. and K. Stattegger. 2000. Lowermost Amazon River: Evidence of late Quaternary sea-level fluctuations in a complex hydrodynamic system. Quatern. Int. 72: 53–60.
Vonhof, H. B., F. P. Wesselingh, and G. M. Ganssen. 1998. Reconstruction of the Miocene western Amazonian aquatic system using molluscan isotopic signatures. Palaeogeogr. Palaeoclimatol. Palaeoecol. 141: 85–93.
Wadge, G. and K. Burke. 1983. Neogene Caribbean plate rotation and associated Central American tectonic evolution. Tectonics 2: 633–643.
Watts, W. A. and B. C. S. Hansen. 1994. Pre-Holocene and Holocene pollen records of vegetation history from the Florida peninsula and their climatic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 163–176.
Weaver, J. N. and G. H. Wood Jr. 1994. Coal Map of South America. U.S. Geological Survey Coal Investigations Map C-145. Pamphlet and Map. Scale 1:7,500,000.
Weber, J. C. et al. (+9 authors). 2001. GPS estimate of relative motion between the Caribbean and South American plates, and geologic implications for Trinidad and Venezuela. Geology 29: 75–78.
Wells, W. B. 1857. Explorations and Adventures in Honduras, Comprising Sketches of Travel in the Gold Regions of Olancho, and a Review of the History and General Resources of Central America. Harper and Brothers, New York.
West, R. C. 1964. Surface Configuration and Associated Geology of Middle America. *In:* R. Wauchope (ed.) and R. C. West (vol. ed.), Handbook of Middle American Indians, Vol. 1: Natural Environment and Early Cultures. University of Texas Press, Austin.
Westgate, J. W. and C. T. Gee. 1990. Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 78: 163–177.
Weyl, R. 1961. Die Geologie Mittelamerikas. Gebrüder Borntraeger, Berlin.
———. 1966. Geologie der Antillen. Gebrüder Borntraeger, Berlin.
———. 1973. Die Paläogeographische Entwicklung Mittelamerikas. Zentrabl. Geol. Paläeont. 5/6: 432–466.
———. 1980. Geology of Central America. 2nd ed. Gebrüder Borntraeger, Berlin.
Whitfield, J. 2004. Time Lords. Nature 429: 124–125.
Williams, R. S., Jr., and J. G. Ferrigno (eds.). 1998. Satellite Image Atlas of Glaciers of the World, Glaciers of South America. U.S. Geol. Surv. Prof. Paper 1386-I.
Winsemann, J. 1994. Origin and tectonic history of the western Caribbean region. *In:* H. Seyfried and W. Hellmann (eds.), Geology of an Evolving Island Arc: The Isthmus of Southern Nicaragua, Costa Rica, and Western Panamá. Profil (Institut für Geologie und Paläontologie, Universität Stuttgart) 7: 1–15.
Wolf, T. 1892. Geografía y Geología del Ecuador. Brockhaus, Leipzig, Germany. [Reprinted 1975, Casa de la Cultura Ecuatoriana, Quito, Ecuador.]
Woodring, W. P. 1928. Tectonic features of the Caribbean region. Proceedings of the 3rd Pan-Pacific Scientific Congress (Tokyo). pp. 401–431.
———. 1954. Caribbean land and sea through the ages. Geol. Soc. Amer. Bull. 65: 719–732.
———. 1966. The Panama land bridge as a sea barrier. Proc. Amer. Philos. Soc. 110: 425–433.
Zeil, W. 1979. The Andes, a Geological Review. Gebrüder Borntraeger, Berlin.

ADDITIONAL REFERENCES/GENERAL READINGS/ ELECTRONIC ADDRESSES

Abels, A. and L. Bischoff. 1999. Clockwise block rotations in northern Chile: Indications for a large-scale domino mechanism during the middle–late Eocene. Geology 27: 751–754.
Alvarez, W. 2001. Eastbound sublithosphere mantle flow through the Caribbean gap and its relevance to the continental undertow hypothesis. Terra Nova 13: 333–337.
Angulo, R. J., P. Giannini, K. Suguio, and L. Pessenda. 1999. Relative sea-level changes in the last 5500 years in southern Brazil (Laguna–Imbituba region, Santa Catarina state) based on vermetid ^{14}C ages. Mar. Geol. 159: 323–339.
Baker, L. (Publications Reviewer). 1988. Transactions of the 11th Caribbean Geological Conference. Energy Division of the Ministry of Finance, Barbados, West Indies.
Bibliography of Caribbean Geology and Geophysics. http://www.ig.utexas.edu/research/projects/plates/biblio/carib/d.htm. Institute for Geophysics, University of Texas, Austin.
Bonatti, E. et al. (+ 7 authors). 2003. Mantle thermal pulses below the Mid-Atlantic Ridge and temporal variations in the formation of oceanic lithosphere. Nature 423: 499–505. [See also accompanying summary, P. D. Asimow, A slice of history, pp. 491–493.]
Briggs, R. P. 1964. Provisional geologic map of Puerto Rico and adjacent islands. U.S. Geol. Surv. Miscell. Geol. Invest. Map I-392.
Bruce, V. 2001. No Apparent Danger: The True Story of Volcanic Disaster at Galeras and Nevado del Ruiz. HarperCollins Publishers, New York. [Account of a 1993 volcanic eruption in Colombia that killed six researchers. See also Williams and Montaigne, 2001 (below), and review by Dalton, 22 March 2001, Nature, Vol. 410, p. 400.]
Camacho, H. H., A. M. Brand, A. Parada, and A. Rimski-Korsakov. 1984. Bibliografía geológica de la Argentina (1980–1981). Publ. No. 1, Centro de Investigaciones en Recursos Geológicos (CIRGEO), Buenos Aires.

———, ———, and ———. 1987. Bibliografía geológica de la Argentina (1982–1983). Publ. No. 2, Centro de Investigaciones en Recursos Geológicos (CIRGEO), Buenos Aires.

Caribbean Geology and Tectonics Web site. Geologic map of Hispaniola. www.fiu.edu/orgs/caribgeol/hispaniola.html.

Charrier, R. et al. (+ 7 authors). 1996. New evidence for late Mesozoic–early Cenozoic evolution of the Chilean Andes in the upper Tinguiririca Valley (35°S), central Chile. J. S. Amer. Earth Sci. 9: 393–422. [Land-mammal fauna.]

Coates, A. G., D. F. McNeil, M.-P. Aubry, W. A. Berggren, and L. S. Collins. 2005. An introduction to the geology of the Bocas del Toro Archipelago, Panama. Caribbean J. Sci. 41: 374–391.

Cordani, U. G., E. J. Milani, A. T. Filho, and D. A. Campos. 2000. Tectonic Evolution of South America. Thirty-first International Geological Congress (Rio de Janeiro, 2000). Geological Society of America, Boulder, CO.

Cyranoski, D. 2003. Digging in. Nature 426: 492–494. [The new Integrated Ocean Drilling Program (IODP).]

Donnelly, T. W. 1988. Geologic constraints on Caribbean biogeography. *In:* J. K. Liebherr (ed.), Zoogeography of Caribbean Insects. Cornell University Press, Ithaca, NY. pp. 15–37.

Donovan, S. K. and T. A. Jackson (eds.). 1994. Caribbean Geology, An Introduction. University of the West Indies Publishers' Association (UWIPA), Kingston, Jamaica.

Erlich, R. N. and S. F. Barrett. 1990. Cenozoic plate tectonic history of the northern Venezuela–Trinidad area. Tectonics 9: 161–184.

Espizua, L. E. 1999. Chronology of late Pleistocene glacier advances in the Río Mendoza Valley, Argentina. Global Planet. Change 22: 193–200.

Ferrari, L., M. López-Martínez, G. Aguirre-Díaz, and G. Carrasco-Núñez. 1999. Space-time parameters of Cenozoic arc volcanism in central Mexico: From the Sierra Madre Occidental to the Mexican Volcanic Belt. Geology 27: 303–306.

Foulger, G. R., J. H. Natland, D. C. Presnall, and D. L. Anderson (eds.). 2005. Plates, Plumes, and Paradigms. Geological Society of America, Boulder, CO. [See review, P. Tackley, 2006, Science 313, pp. 1240–1241.]

GOES 9/10/12 Hotspot Images Web site. http://goes.higp.hawaii.edu/goes.shtml. Hawaii Institute of Geophysics and Planetology, University of Hawaii.

Graham, A. 2009. The Andes: A geological overview from a biological perspective. Ann. Missouri Bot. Gard. 96: 371–385.

Herbert, S. 2005. Charles Darwin, Geologist. Cornell University Press, Ithaca, NY. [See review by P. Lucier, Amer. Sci., Jan–Feb., 2006.]

Isla, F. I., L. C. Cortizo, and E. J. Schnack. 1996. Pleistocene and Holocene beaches and estuaries along the southern barrier of Buenos Aires, Argentina. Quatern. Sci. Rev. 15: 833–841.

Jablonski, D. 2004. Extinction: Past and present. Nature 427: 589.

Johnson, M. E., J. Ledesma-Vázquez, H. C. Clark, and J. A. Zwiebel. 1996. Coastal evolution of Late Cretaceous and Pleistocene rocky shores: Pacific rim of northern Baja California, Mexico. Geol. Soc. Amer. Bull. 108: 708–721.

Jones, N. 2003. How do your mountains grow? Nature 425: 781.

Keller, G., J. G. Lopez-Oliva, W. Stinnesbeck, and T. Adatte. 1997. Age, stratigraphy, and deposition of near-K/T siliciclastic deposits in Mexico: Relation to bolide impact? Geol. Soc. Amer. Bull. 109: 410–428.

Kennan, L., S. Lamb, and C. Rundle. 1995. K-Ar dates from the Altiplano and Cordillera Oriental of Bolivia: Implications for Cenozoic stratigraphy and tectonics. J. S. Amer. Earth Sci. 8: 163–186.

Kerr, R. A. 2005. Scientific drill ship to be reborn. Science 310: 1890–1891.

———. 2006. An early date for raising the roof of the world. Science 311: 758.

Kölbl-Ebert, M. 1999. Observing orogeny—Maria Graham's account of the earthquake in Chile in 1822. Episodes Int. Geosci. Newsmagazine 22: 36–40.

Kröhling, D. M. 1999. Sedimentological maps of the typical loessic units in north pampa, Argentina. Quatern. Int. 62: 49–55.

Kruckeberg, A. R. 2002. Geology and Plant Life: The Effects of Landforms and Rock Types on Plants. University of Washington Press, Seattle.

Lamb, S. and D. Sington. 2003. Earth Story: The Forces that Have Shaped Our Planet. Princeton University Press, Princeton, NJ.

Larue, D. K. and G. Draper (eds.). 1990. Transactions 12th Caribbean Geological Conference, St. Croix, U.S. Virgin Islands. Miami Geological Society, Miami.

Lidz, B. and F. Nagle (eds.). 1979. Hispaniola: Tectonic Focal Point of the Northern Caribbean–Three Geologic Studies in the Dominican Republic. Miami Geological Society, Miami. [Papers by F. Nagle, N. C. Palmer, and G. A. Antonini.]

Love, S. P., F. Goff, D. Counce, C. Siebe, and H. Delgado. 1998. Passive infrared spectroscopy of the eruption plume at Popocatépetl volcano, Mexico. Nature 396: 563–567.

Machel, H. G. 1999. Geology of Barbados—a Brief Account of the Island's Origin and its Major Geological Features. Barbados Museum and Natural History Society, St. Michael, Barbados, West Indies.

Mann, P., F. W. Taylor, K. Burke, and R. Kulstad. 1984. Subaerially exposed Holocene coral reef, Enriquillo Valley, Dominican Republic. Geol. Soc. Amer. Bull. 95: 1084–1092.

McElwain, J. C. and S. W. Punyasena. 2007. Mass extinction events and the plant fossil record. Trends Ecol. Evol. 22: 548–557.

Mégard, F. 1987. Structure and evolution of the Peruvian Andes. *In:* J.-P. Schaer and J. Rogers (eds.), The Anatomy of

Mountain Ranges. Princeton University Press, Princeton, NJ. pp. 179–210.
Melosh, H. J. 1995. Around and around we go. Nature 376: 386–387. [Debate on the size of the K/T asteroid.]
Montgomery, D. R., G. Balco, and S. D. Willett. 2001. Climate, tectonics, and the morphology of the Andes. Geology 29: 579–582.
Muñoz, N. and R. Charrier. 1996. Uplift of the western border of the Altiplano on a west-vergent thrust system, northern Chile. J. S. Amer. Earth Sci. 9: 171–181.
Murphy, J. B. and R. D. Nance. 2004. How do supercontinents assemble? Amer. Sci. 92: 324–333.
Newell, N. D. 1949. Geology of the Lake Titicaca region, Peru and Bolivia. Geol. Soc. Amer. Mem. 36: 1–111.
Nichols, D. J. 2007. The Chicxulub impact event and its environmental consequences at the Cretaceous–Tertiary boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 255: 4–21.
Noble, D. C., E. H. McKee, T. Mourier, and F. Mégard. 1990. Cenozoic stratigraphy, magmatic activity, compressive deformation, and uplift in northern Peru. Geol. Soc. Amer. Bull. 102: 1105–1113.
Norabuena, E. et al. (+ 7 authors). 1998. Space geodetic observations of Nazca–South America convergence across the central Andes. Science 279: 358–362.
Nyblade, A. A. 2001. Hard-core continents. Nature 411: 38–39.
Ocean Drilling Stratigraphic Network Plate Tectonic Reconstruction Service. http://www.odsn.de/odsn/services/paleomap/paleomap.html.
Oncken, O. et al. (+ 7 eds.). 2006. The Andes: Active Subduction Orogeny. Frontiers in Earth Sciences. Springer Verlag, Berlin.
PALEOMAP Project Web site. http://www.scotese.com. [Information on availability of paleogeographic atlas and sea floor spreading as CDs, slides, and animations.]
Panario, D. and O. Gutiérrez. 1999. The continental Uruguayan Cenozoic: An overview. Quatern. Int. 62: 75–84. [See also comment, M. Ubilla, 2001, 76/77: 259–260.]
Poage, M. A. and C. P. Chamberlain. 2006. Raising mountain ranges. Science 311: 478–479.
Porter, A. R. D. 1990. Jamaica: A Geological Portrait. Institute of Jamaica Publications, Kingston, Jamaica.
Rice, P. C. 1993. Amber: The Golden Gem of the Ages. The Kosciuszko Foundation, New York.
Robinson, D. P., S. Das, and A. B. Watts. 2006. Earthquake rupture stalled by a subducting fracture zone. Science 312: 1203–1205. [Mechanics of the 23 June 2001 earthquake of 8.4 magnitude, Arequipa, Peru.]
Rostami, K., W. R. Peltier, and A. Mangini. 2000. Quaternary marine terraces, sea-level changes and uplift history of Patagonia, Argentina: Comparisons with predictions of the ICE-4G (VM2) model of the global process of glacial isostatic adjustment. Quatern. Sci. Rev. 19: 1495–1525.
Roux, J. P. le, C. Tavares Correa, and F. Alayza. 2000. Sedimentology of the Rímac-Chillón alluvial fan at Lima, Peru, as related to Plio–Pleistocene sea-level changes, glacial cycles and tectonics. J. S. Amer. Earth Sci. 13: 499–510.
Rowley, D. B. and C. N. Garsione. 2007. Stable isotope-based paleoaltimetry. Ann. Rev. Earth Planet. Sci. 35: 463–508.
Rudwick, M. J. S. 2005. Bursting the Limits of Time: The Reconstruction of Geohistory in the Age of Revolution. University of Chicago Press, Chicago. [See review, Nature 2006, vol. 444: 743.]
Santiago-Blay, J. A. and J. B. Lambert. 2007. Amber's botanical origins revealed. Amer. Sci. 95: 150–157.
Saunders, J. B., P. Jung, and B. Biju-Duval. 1986. Neogene paleontology in the northern Dominican Republic. Part 1. Field surveys, lithology, environment, and age. Bull. Amer. Paleontol. 89: 1–79.
Scheuber, E. and P. Giese. 1999. Architecture of the Central Andes—A compilation of geoscientific data along a transect at 21°S. J. S. Amer. Earth Sci. 12: 103–107.
Schubert, C. 1982. Origin of Cariaco Basin, southern Caribbean Sea. Mar. Geol. 47: 345–360.
Servant, M. et al. (+ 5 authors). 1989. Morphogenèse et soulèvement de la Cordillère Orientale des Andes de Bolivie au Cénocoïque. Compt. Rend. Acad. Sci. Paris 309: 417–422.
Silver, R. G., R. M. Russo, and C. Lithgow-Bertelloni. 1998. Coupling of South American and African plate motion and plate deformation. Science 279: 60–63.
Simkin, T. et al. (+ 5 authors). 2006. This Dynamic Planet: World Map of Volcanoes, Earthquakes, Impact Craters, and Plate Tectonics. U.S. Geological Survey, Smithsonian Institution, and U.S. Naval Research Laboratory, Washington, D.C. [U.S. Geological Survey Investigations Series Map I-2800; see review, P. Crowley, Science 2006, vol. 313, p. 1241.]
Somoza, R. 1998. Updated Nazca (Farallon)–South American relative motions during the last 40 My: Implications for mountain building in the central Andean region. J. S. Amer. Earth Sci. 11: 211–215.
Stinnesbeck, W., G. Keller, and T. Adatte. 2001. Chicxulub impact: The origin of reservoir and seal facies in the southeastern Mexico oil fields: Comment. Geology 29: 94–95. [See Reply, Grajales-Nishimura et al., pp. 95–96.]
Stratigraphy and Sedimentology on the Colorado Plateau. http://jan.ucc.nau.edu/~rcb7/. [Paleogeographic maps and links to other Web sites.]
Tarling, D. H. 1997. The plate tectonic impact on climatic change with particular relevance to Mesoamerica. Quatern. Int. 43/44: 61–66.
Twitchett, R. J. 2006. The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 232: 190–213.
Veblen, T. T., K. R. Young, and A. R. Orme (eds.). 2007. The Physical Geography of South America. Oxford University Press, Oxford, U.K.
Vergniolle, S. 1997. Listening to Pele. Science 275: 1278–1279.

Voight, B. et al. (+ 24 authors). 1999. Magma flow instability and cyclic activity at Soufrière Hills volcano, Montserrat, British West Indies. Science 283: 1138–1142.

Wadge, G. and T. H. Dixon. 1984. A geological interpretation of SEASAT-SAR imagery of Jamaica. J. Geol. 92: 561–581. [Includes an overview of the surface features of Jamaica, p. 563.]

Warren, C. and M. Aniya. 1999. The calving glaciers of southern South America. Global Planet. Change 22: 59–77.

Williams, S. and F. Montaigne. 2001. Surviving Galeras. Houghton Mifflin, Boston.

Yuan, X. et al. (+ 21 authors). 2000. Subduction and collision processes in the Central Andes constrained by converted seismic phases. Nature 408: 958–961.

Zebrowski, E., Jr. 2002. The Last Days of St. Pierre: The Volcanic Disaster that Claimed 30,000 Lives. Rutgers University Press, New Brunswick, NJ.

Chapter 3

VEGETATION

Classification

The number of species on Earth is unknown, but a new round of estimates was ushered in with Terry Erwin's (1982) calculation that there may be as many as 30 million different kinds of arthropods alone, while extrapolations from that number yielded figures as high as 50,000,000 eukaryotic species. This number has been scaled down to about 6,800,000 to 12,200,000 eukaryotes (Hammond, 1995; May 1997), of which only ~1,500,000 have been named. The impact of Erwin's widely publicized estimate was to renew interest in determining the actual number for purposes of conservation (Raven, 1997; Pimm & Raven, 2000; Wilson & Perlman, 2000; Pimm, 2001), the identification of biodiversity "hotspots" (Mittermeier et al., 2000; Myers et al., 2000; Myers, 2003), and recognition of sensitive ecoregions.[1] The most ambitious of the inventory programs is the developing megaproject Encyclopedia of Life. For vascular plants, the figures range from ~320,000 to >400,000 species (Govaerts, 2001; Ungricht, 2004; Chapman, 2005), with about 50,000 remaining to be described (Table 3.1).

In Latin America, the vast array of habitats, the dynamic histories of climate and landscape, and migratory, speciation, and evolutionary-extinction processes have produced a net biota of unparalleled richness and complexity. There are about 100,000 to 110,000 species of flowering plants in the Neotropics, in addition to lichens, bryophytes, ferns and allied groups, gymnosperms, and an undetermined number of algae, fungi, and other microorganisms. These estimates are conservative, however, because only two countries in South America, Peru and Ecuador, have relatively complete lists of native plants. As additional inventories are completed, estimates of diversity become more accurate, and some unexpected results are emerging. Globally about 22% to 27% of plant species are threatened, and among these, endemics are particularly important because of their limited distribution. When the recent catalogs and checklists for Ecuador were analyzed, an astonishing 83% of the endemic plant species qualified as threatened (Pitman & Jørgensen, 2002).

Table 3.1. Estimated total number and described number of living species of eukaryotes (data from May 1997).

Group	Total number living species	Described number living species
Protozoa	100,000	40,000
Algae	300,000	40,000
Plants	320,000	270,000
Fungi	500,000	70,000
Animals		
Vertebrates	50,000	45,000
Nematodes	500,000	15,000
Molluscs	120,000	70,000
Arthropods		
Crustaceans	150,000	40,000
Arachnids	500,000	75,000
Insects	4,000,000	720,000
Total arthropods	4,650,000	835,000
Other animals	250,000	115,000
Total animals	5,570,000	1,080,000
TOTAL	6,790,000	1,500,000

Within this diversity, there are recognizable clusters of vegetation resulting from similarities in evolutionary histories and ecological requirements, particularly climate, and from a myriad of additional factors such as soil requirements, interaction with other organisms (e.g., pollinators), and past geologic events. These have determined the composition and have produced the spatial arrangements evident in modern assemblages. For purposes of biogeography, paleoecology, and biotic history, these groupings must be named and broadly characterized. Vegetation is the most visible, enduring, and fixed component of the living landscape, and it is used to classify the Earth's plant and animal assemblages into biotic formations. The early attempts by Humboldt (1807), Schimper (1903), and Warming (1909) were improved for tropical regions with the arrangement of forest trees by physiognomy (height, number of canopy layers), accompanied by profile diagrams (Richards, 1936; Richards et al., 1940; Davis & Richards, 1933–1934; see e.g., Figs. 3.31, 3.52), and by Barbour's (1942) efforts to standardize the nomenclature used to describe primary forest types in tropical America. However, the systems were frequently modified and used by various authors for diverse purposes, so that when Beard (1944, p. 127) sought one applicable to the plant communities of Trinidad and Tobago, he found that "…nomenclature and classification of tropical vegetation are unfortunately in great confusion" (see also Beard, 1955; Table 3.2).

A system widely used for classifying Latin American climates and the associated vegetation types was developed by Holdridge (1947a; Tosi, 1964; Sawyer & Lindsey, 1971; Fig. 3.1). It is based on the relationship between latitudinal and altitudinal variations in climate and the distribution of communities or

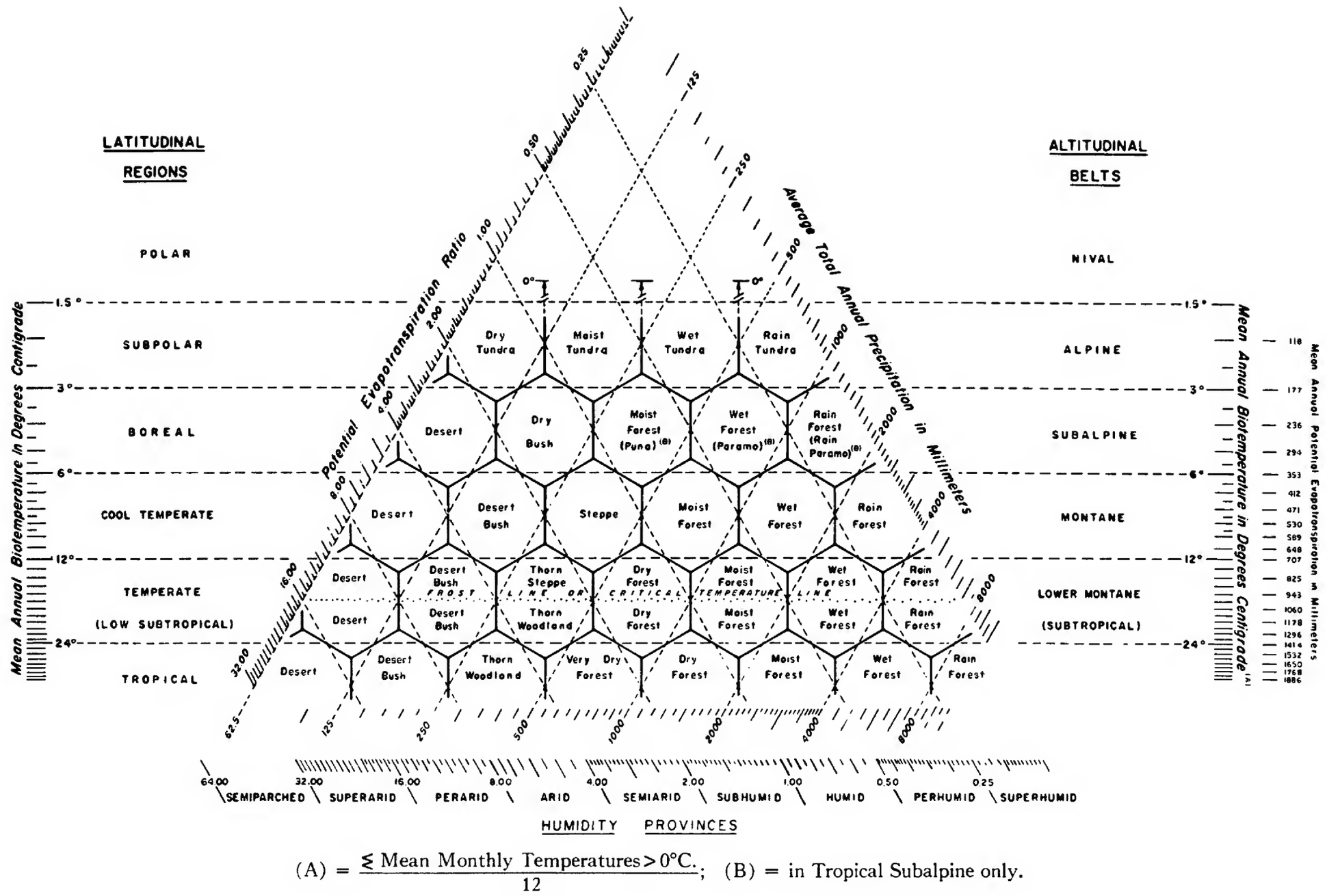
Table 3.2. An early effort at classifying the vegetation of tropical America (first column) and providing the English, Spanish, and Portuguese equivalents of the plant formation names (Beard, 1944; see also Beard, 1955). Revised Portuguese nomenclature provided by Taciana Cavalcanti and Bruno M. T. Walter (pers. comm., 2006).

English	Spanish	Portuguese
NON-SEASONAL FORMATIONS		
Rain forest	selva pluvial	mata/floresta pluvial
SEASONAL FORMATIONS		
Evergreen seasonal forest	selva veranera siempreverde	mata/floresta estacional sempre-verde
Semi-evergreen seasonal forest	selva veranera semidecidua	mata/floresta estacional semidecídua
Deciduous seasonal forest	selva veranera decidua	mata/foresta estacional decídua
Thorn woodland	espinar	mata/arvoredo espinhoso
Cactus scrub	cardonal	"escrube de cactus"*
Desert	desierto	deserto
DRY EVERGREEN FORMATIONS		
Xerophytic rain forest	selva pluvial xerofítica	mata/floristica pluvial xerofítica
Littoral woodland	bosque de playa	arvoredo/mata litorânea
MONTANE FORMATIONS		
Lower montane rain forest	selva pluvial intermédia	mata/floresta pluvial submontana
Montane rain forest	selva nublada	mata/floresta pluvial montana
Palm brake	matorral de palmeras, manacal	bosque de palmeiras, palmeiral
Elfin woodland	bosque eneano	arvoredo/mata baixa
Frost woodland	bosque de helada	"arvoredo/mata de geada"*
Mountain pine forest	pinar de montaña	mata/foresta montanhosa de pinheiros
Bamboo brake	bamboal	bosque de bambus, bambuzal
Páramo	páramo	páramo
Tundra	tundra	tundra
SWAMP FORMATIONS		
Swamp forest	selva de pantano	mata/floresta pantanosa (inundável)
Palm swamp	pantano de palmeras	pântano de palmeiras, palmeiral, pantanoso*
Herbaceous swamp	pantano herbáceo	pântano herbáceo, "brejo"
Mangrove woodland	manglar	manguezal, mangue
MARSH OR SEASONAL SWAMP FORMATIONS		
Marsh forest	selva de lodazal	mata/floresta brejosa (de brejo)
Marsh woodland	bosque de lodazal	arvoredo/mata brejosa (de brejo)
Palm marsh	lodazal con palmeras, morichal	brejo de palmeiras, palmeiral brejoso**
Savanna	sabana	savana

* Literal translation, without a direct Portuguese equivalent.
** No semantic difference.

life zones over the landscape. Among the expectations of this relationship are that (1) given the vegetation for a region, it should be possible to predict the general climate, and (2) given the climatic data, it should be possible to predict the life zones that will be present. In a broad sense, this has proven to be the case. The diagram is constructed by using precipitation, temperature, and precipitation/evaporation (P/E) values to form a grid of hexagons. Each hexagon represents a life zone, and the triangular areas outside the hexagons are transition zones. Other factors that affect vegetation, such as soil and topography, are more local in importance and serve to subdivide the formations into associations. The names assigned to the life zones are based primarily on altitude, moisture, and vegetation type (e.g., lower montane rain forest, montane wet forest, subalpine desert). The scheme, which has been used to classify vegetation in many parts of the world, is the one adapted by the United Nations' Food and Agriculture Organization for this purpose, and the names are frequently encountered in the literature even if not as defined in the Holdridge system. However, Walsh (1996, pp. 164–165) believes one assumption, namely, that any temperature above 30° C can be reduced to 30° C in calculating the biotemperature, is dubious and that a more serious flaw is that the system does not take into account seasonality and length of the dry season. He concludes that "the life zones and their boundaries appear to be highly arbitrary and the system has not proved useful in climate-ecological mapping in the tropics as a whole" (see also Shuttleworth et al., 1984). Even so, it is still widely used in a broad and variable sense.

For the present treatment, several criteria were used to



$$(A) = \frac{\leq \text{Mean Monthly Temperatures} > 0°\text{C.}}{12}; \quad (B) = \text{in Tropical Subalpine only.}$$

Figure 3.1. Holdridge classification of world plant formations (natural life zones; Tosi, 1964; Hartshorn, 1983, pp. 119–121). Used with permission of the Tropical Science Center, San José, Costa Rica.

develop a classification system for the various modern Latin American vegetation types appropriate, specifically, to a discussion of their history. One was that, as far as possible, the categories should be sufficiently broad to cover similar vegetation across geographic, political, and language boundaries. The term "lowland Neotropical rain forest" is used here to designate the community throughout its range, although in Latin America it is known by several names. At its northern limit in Veracruz, Mexico, it is called the bosque tropical perennifolio and the selva alta perennifolia; in Central America the tropical wet forest; and in the Amazon Basin of South America the floresta tropical húmida. Similarly, the vegetation formation in Mexico designated as the bosque tropical subcaducifolio (tropical semi-deciduous woodland) is also known by 16 other names (Rzedowski, 1978, pp. 179–180). In Beard's (1944) classification (Table 3.2), many of his "Spanish equivalents" are not equivalent, and it does not include the units added by later authors (e.g., Miranda and Hernández X., 1963, Rzedowski, 1978 for Mexico; Gómez-Pompa, 1973 for Veracruz; UNESCO, 1980–1981 for South America).

It is inevitable that difficulties in definition and a proliferation of names will arise when a system of classification is imposed on natural communities in different stages of maturity, states of preservation, phases of successional development, and frequently with broad ecotones between them. Also, different aspects of the vegetation are often selected for emphasis depending on the purpose of the classification. In the example of the lowland Neotropical rain forest, one name (selva alta perennifolia) is based on the height and deciduousness of the trees, and this is convenient for forestry and photogrammetry (forest mapping). Another name (floresta tropical húmida) uses humidity in defining the community, and this better serves some purposes in ecology. From the mélange of systems and terms, it is necessary to assemble one that is applicable, to the extent possible, to vegetation types throughout their range in Latin America.

A second criterion is that the system must accommodate the units and concepts of paleovegetation analysis, paleoecology, and ecosystem evolution; that is, it must be suitable for a discussion of vegetation history and be applicable to the ancient analogs from which the modern assemblages were derived. Schemes emphasizing generic composition are useful because identification is the usual first step in paleobotanical studies. The pine-oak woods (bosque de pino y encino) and the high-altitude fir forests (bosque de oyamel) are defined by the presence of the dominants *Pinus–Quercus* and *Abies*, and each of these genera is known in the fossil record of Latin America.

Third, the complexity of the system need only be commensurate with the general nature of paleocommunity reconstructions. In Veracruz, the height of tropical forest trees decreases and the extent of deciduousness gradually increases with declining moisture. Thus, it is possible to recognize a tall semi-evergreen forest (selva alta subperennifolia), medium semi-evergreen forest (selva mediana subperennifolia), medium deciduous forest (selva mediana caducifolia), low semi-evergreen forest (selva baja subperennifolia), and low deciduous forest (selva baja caducifolia; Gómez-Pompa, 1973). To the extent that these are distinguished by different genera, they are useful for describing past vegetation. Usually, however, the differences are too subtle to be recognized in fossil floras. Similarly, the cerrado (more or less savanna to open woodland) of Brazil can be subdivided into an almost infinite number of phases resulting from variations in climate (MAT, MAP, length and extent of seasonal extremes), soil (chemistry, pH, depth, texture, color, albedo, evapotranspiration potential), slope, exposure, drainage, stage of recovery from disturbance, and a host of other factors. These local variants are important for understanding local community dynamics, and they hold a great fascination for the specialist. But the intricate nomenclature is not appropriate for an introduction to the vegetation, it can be counterproductive to achieving a general understanding of the cerrado, and it is not applicable to paleocommunities.

Fourth, the extent to which each community is discussed must balance between providing an adequate description of the vegetation, and the eventual relevancy of the information to vegetation history. Some lineages and communities are not well represented in the fossil record; some geographic regions, or even entire countries, contain no recently studied fossil floras; and paleobotanical information is often lacking for major segments of geologic time. They are consequently less relevant for present purposes than those for which an extensive paleobotanical record exists. For example, the desert is an important part of modern Latin American vegetation, including the Sonoran and Chihuahuan deserts of Mexico, the Atacama Desert of Chile, and the near-desert Monte of Argentina, but the pre-late Quaternary history of deserts is poorly known because most plant remains do not preserve well under arid environments, and there are few drainage systems suitable for transporting the remains into basins of deposition. There is little data for the Late Cretaceous and Cenozoic of the Lesser Antilles, Belize, El Salvador, Honduras, Nicaragua, the Guianas, Paraguay, Peru, or Uruguay, while more information exists for Mexico, the Greater Antilles, Costa Rica, Guatemala, Panama, Argentina, Bolivia, Brazil, Chile, Colombia, and Venezuela. The extent of the treatment of modern communities here must be, in part, a reflection of whether the information will be used later for discussing vegetation history.

Fifth, the terminology must facilitate, rather than impede, an understanding of the vegetation for a broad audience that includes general readers as well as specialists. Thus, the names for many of the plant formations used here are those in the international literature (e.g., tundra, desert, grassland), which have been further standardized by recent usage (e.g., Barbour & Billings, 2000; Flora of North America Editorial Committee, 1993 et seq.). This allows a transition to the numerous, more complex, regional and linguistic-based classifications applied to Mexico, the Antilles, and Central America. To the extent possible, a similar nomenclature is used for South America, but it must be somewhat specific to this region. During its ~30 Ma isolation as an island continent, South America developed communities unique in composition and extent, and the system must reflect this distinctiveness (e.g., pantanal for the vast wetlands of the southern Brazil region; várzea for the extensive floodplain forests of the Amazon lowlands; chocó for the region and vegetation of northwestern Colombia with almost perpetual rain).

The goals are to apply a uniform classification system as widely and consistently as possible to the modern vegetation of Latin America. It must be comprehensible to a broad audience, suitable for tracing its Late Cretaceous and Cenozoic history, and adequate for describing the biological and environmental events that drove the process. The communities either must be recognizable in the fossil record, or ones that can be inferred from that record when augmented by global and regional context information. This specific approach avoids the elusive and probably futile quest for a system suited for all purposes, and applicable to every component of an ancient and dynamic biotic continuum with its unparalleled complexity and diversity.

The system developed for these purposes recognizes 12 plant formations that can be subdivided as necessary into associations and into more local phases representing concentrations of edaphically or microclimate-controlled assemblages (e.g., stands of ferns, bamboos, palms), and disturbed or seral phases (e.g., stands of *Cecropia*) often found within the broader vegetation. These formations are:

Desert
Shrubland/chaparral–woodland–savanna
Grassland
Mangrove (including mudflat association marginal to the habitat)
Beach/strand/dune
Freshwater herbaceous bog/marsh/swamp (including associated woody species ranging into the swamps from adjacent vegetation)
Aquatic
Lowland Neotropical rain forest
Lower to upper montane broad-leaved forest
Coniferous forest
Páramo (alpine tundra)
Tundra

The aspects of modern vegetation most relevant to reconstructing regional histories are (1) the plant formations present, (2) their distribution, (3) composition, with emphasis on the prominent or defining genera and species, (4) general environments under which they grow, (5) likelihood of preservation

under the environments they represent, and (6) the spore and pollen signature of the modern communities. This signature is defined as the kind and amounts of spores and pollen released by a vegetation type, and which are potentially available for transport by wind, water, and animals into basins of deposition. It is determined by studying the modern spore and pollen rain within the vegetation and onto bogs, lake surfaces, moss polsters, and cattle tanks in relation to the surrounding vegetation and by sampling the atmosphere, river water, and recent sediments (e.g., near-shore marine and delta deposits) for the microfossils preserved. Identifications are facilitated when reference collections and catalogs are available for the regional vegetation (e.g., *Pollen and Spores of Barro Colorado Island*, Roubik & Moreno P., 1991), and these are mentioned at appropriate places in the text.

In Appendix 1, the plant formations used in the text are listed with representative species. In perusing the list, it will be evident that certain taxa are frequently recorded as fossils (Appendix 2), while others are not. This gives an indication of the potential for tracing specific lineages and communities based on paleobotanical evidence, and it reveals the strengths and limitations of the various methodologies. For example, leaves of the Lauraceae are often reported as megafossils, while microfossils are not encountered because the unique chemistry of the pollen wall precludes their fossilization. In contrast, the leaves of annuals wilt on the stem and are almost never found as megafossils, but the pollen is often abundant (I: ch. 4).

A valuable resource on the composition of plant formations in tropical America is Gentry's Forest Transect Data Set (Phillips & Miller, 2002). This sampling technique involves collecting representatives of every species of vascular plants ≥2.5 cm dbh from 10 transects each 2 × 50 m (0.1 ha) in size (Gentry plots). The system is now widely used, and for the first time biodiversity is being measured by a standard method. Thus, when it is stated that Neotropical forest diversity ranges up to 276 species/ha, compared to an average of 20 species/ha for the temperate forests of North America, it is with the confidence that the same sampling method was used for both calculations.

Another valuable contribution of Gentry's method is that it allows a rapid estimate of diversity for establishing conservation priorities for species (International Union for Conservation of Nature and Natural Resource's Red List) or areas under imminent threat. The Rapid Assessment Program (RAP) used by Conservation International to focus on unusually species-rich areas utilizes the 0.1-ha transect method. The ability to identify sterile material is essential in tropical botany, and Gentry developed keys based on vegetative characters (Gentry, 1993; Keller, 1996). Given the luxury of reproductive material, it is said he could recognize the majority of Neotropical trees and shrubs.

Alwyn Gentry was killed in an airplane crash on 3 August 1993 in Ecuador. Also killed in the crash were Conservation International ornithologist Theodore Parker III and three others. Parker could recognize 4000 species of birds by their call alone, and this was invaluable for making inventories of threatened areas. The loss of these people created a huge void in the study of tropical biology, and when one recalls the deaths of Gary Polis and his colleagues in the Sea of Cortez and the six researchers killed at Galeras Volcano in Colombia (Dickson, 1993; Bruce, 2001; Williams & Montaigne, 2001; see reviews by Rose, 2001; Sigurdsson, 2001), it is clear that gathering scientific information in tropical regions comes at a price. The Gentry Transect Data Set published by Phillips and Miller (2002) includes the protocol and associated data for the plots, and it is available through the Missouri Botanical Garden Web site (http://www.mobot.org/mobot/research/gentry/transect.shtml).

For the general reader, the scientific names of unfamiliar plants and the wide array of vegetation types and associated terminology can be formidable obstacles to achieving an understanding of the arrangement, composition, and ecology of the plant communities of Latin America. Even the greatest of minds can be daunted:

> "After a separation of six years, Wilhelm [von Humboldt] was overjoyed at seeing Alexander. He wrote to a friend of Schiller: My brother's visit was remarkably pleasant and deeply stirring. Even for me, who keeps natural science at arm's length… his company was so attractive because he always moves in the orbit of his knowledge, but never on its peripheries. He really attempts to embrace all in order to explore one thing, which can be done only by approaching it from all sides. He maintains a horror for the single fact—hence his disdain for botanical nomenclature." (Quoted from de Terra, 1955, p. 229)

It is equally true, however, that achieving a broad concept of the modern Latin American vegetation is essential for envisioning the assemblages as they migrated, recombined, and evolved in response to environmental change. Several approaches are used here to aid in the process. One is that only a representative number of plants are mentioned in the text to illustrate the various vegetation types. More lengthy lists useful for comparing the plant formations throughout their range and for placing fossils in the proper paleocommunity (as leads for the identification of the fossils and as a basis for establishing reference collections) are placed separately in Appendix 1.

For the general reader, further familiarity with tropical vegetation may be gained by periodically consulting electronic sources of illustrations to supplement those included in the text. The first plant mentioned in the discussion of Mexican vegetation is *Larrea tridentata* (creosote bush). By searching the internet for creosote bush, several sites are found that provide a description of the plant and an image of creosote bush in its natural habitat (e.g., Encarta Concise Encyclopedia article). A search for *Agave* (century plant) yields the site Cacti Canyon (http://www.cactus-mall.com) with images of *Agave*, *Opuntia* (prickly pear, cholla cactus), *Ferocactus* (a barrel cactus),

Fouquieria (ocotillo), and *Yucca* (Spanish bayonet), all of which are mentioned in the text. Similar information is available for mangroves, tropical rain forest, cerrado, and other plant formations at innumerable Web sites.

Other sources of illustrations for tropical plants are virtual herbaria. One is the Virtual Herbarium of the New York Botanical Garden (http://sciweb.nybg.org/science2/VirtualHerbarium.asp). Among the catalogs provided at this site are Coastal Forest Plants of Bahia, Ericaceae of Ecuador, Flora of Navassa Island (located between Cuba, Haiti, and Jamaica), Plant Diversity of Central French Guiana, West Indian Orchids, and West Indian Vascular Plant Types. Under Coastal Forest Plants of Bahia there is a link that provides images of many plants mentioned here in the section on South American vegetation. NY is also compiling a catalog of the vascular plants of eastern Brazil (http://sciweb.nybg.org/science2/hcol/sebc/sebcindex2.asp). Other virtual herbaria are being developed at the Fairchild Tropical Gardens (http://www.virtualherbarium.org) and elsewhere.

The TROPICOS database at MO (http://www.tropicos.org) as of September 2007 contained 1,008,141 names, 3,406,030 records, and 111,521 bibliographic entries. The Virtual Herbarium at MO has 70,111 digital images, and includes software for generating distribution maps from locality data. A synopsis of angiosperm families and genera with illustrations is available at http://www.mobot.org/mobot/research/apweb/welcome.html. Similar information is available for the herbarium collections at Harvard University, the U.S. National Herbarium of the Smithsonian Institution, and the Royal Botanic Garden at Kew (see Electronic Addresses under References). Efforts are under way to link these into a single, searchable database. These are impressive examples of the technology now being used to store and retrieve information valuable to biogeography and paleobotany based on herbarium collections. The addresses and the contents for many sites change frequently, but an increasing number of electronic databases are maintained and are permanently available. There is no substitute for field experience to gain knowledge of the biota, including instruction at the several biological stations in Latin America (Whitesell et al., 2002), but as a preliminary exercise, the increasing number of electronic illustrations may be used by general readers to bring greater meaning to the plants, communities, terms, and descriptions encountered in the text.

MEXICO

The number of vascular plant species estimated for Mexico is ~20,000 (Rzedowski, 1978, p. 73; 21,300–24,600, Espejo-Serna et al., 2004). No one system is used consistently, but three schemes have been widely applied (Leopold, 1950; Miranda & Hernández X., 1963; Rzedowski, 1978; Fig. 3.2), and others have been proposed for individual regions (e.g., Veracruz, Gómez-Pompa, 1973; Chiapas, Breedlove, 1973, 1981; Nueva Galicia [Jalisco and surrounding areas], Rzedowski & McVaugh, 1966; and the Valle de México, Rzedowski & de Rzedowski, 1979, 1985, 1990). In the following discussion, a general overview of the vegetation is presented , based primarily on Rzedowski (1978), followed by more detailed reviews for Veracruz and Chiapas, where a number of fossil floras are found and where several modern plant formations are similar to the paleocommunities. The dry vegetation is described first, followed by summaries of coastal through high-elevation communities. Plant fossils reported for the Late Cretaceous and Cenozoic of Mexico are given in Table 4.1 and in Appendices 2.1 and 2.2.

Desert (matorral xerófilo)—This is the arid vegetation of Mexico, although it does not quite meet the conventional definition of a desert where the annual precipitation is ~250 mm (10 in) or less, and where there is an evapotranspiration deficit throughout most of the year. The driest regions of Mexico receive 300–350 mm (12–14 in) per year and support humid deserts or dry shrubland. Associations often recognized within the matorral xerófilo include the matorral desértico micrófilo (the microphyllous desert shrub of *Larrea tridentata*, creosote bush), the matorral desértico rosetófilo (characterized by plants with the rosette form of leaves; e.g., *Agave*), and the matorral crasicaule (characterized by numerous succulent plants such as Cactaceae, and *Yucca*).

Most of Baja California, the adjacent northwestern mainland, and north-central Mexico are covered by desert or matorral xerófilo. It constitutes ~40% of the vegetation cover of the country and includes the Mexican portion of the Sonoran Desert as defined by Shreve (in Shreve & Wiggins, 1964),[2] the Chihuahuan Desert, and a narrow extension southward through the state of San Luis Potosí to the vicinity of Tehuacán in the state of Puebla (Rzedowski, 1973; Fig. 3.2). On the western side of the Sierra de la Giganta, *Bursera hindsiana* and *Jatropha cinerea* are important members, along with *Cercidium microphyllum* and the cacti *Pachycereus pringlei*, *Opuntia*, and *Ferocactus*. The desert along the middle section of the Pacific coast extending inland to the mountain slopes is characterized by *Agave*,[3] *Ambrosia chenopodiifolia*, *Atriplex magdalenae*, *A. polycarpa*, *Idria columnaris*, *Machaerocereus gummosus*, *Pachycormus discolor*, and *Yucca valida*. There are extensive sand dunes, salt flats, and lichen-covered rocks with *Tillandsia*. Climatic data for La Paz in southern Baja California are given in Table 1.2, and a list of biosphere reserves and national parks for the northern states of Mexico is given in Cartron et al. (2005, pp. 4–7).

Associations of the shrubland/chaparral–woodland–savanna formation occupy parts of southeastern Baja California. A shrubland or thicket has a dense, nearly continuous cover of low trees to shrubs; chaparral is a shrubland with a

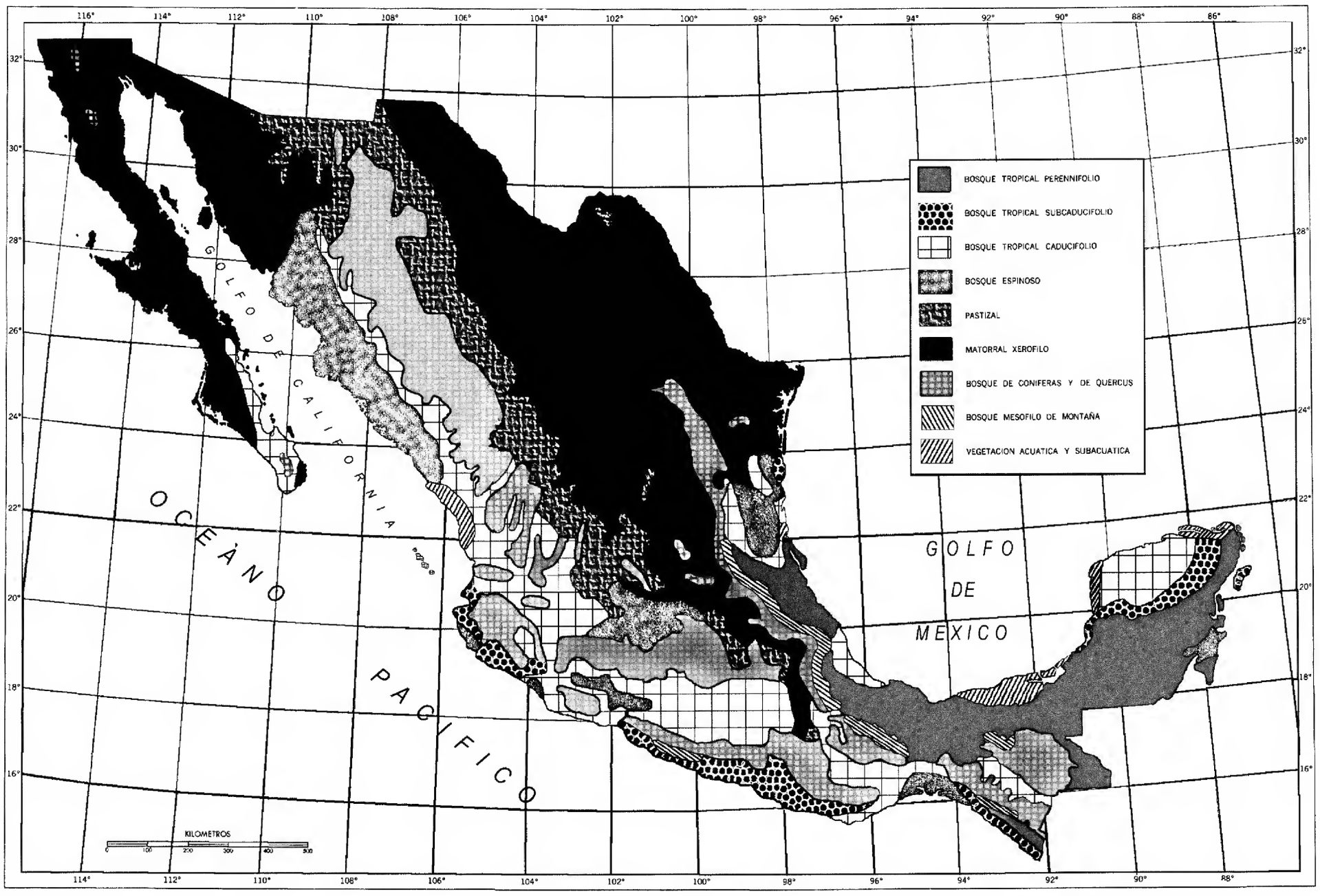


Figure 3.2. Vegetation map of Mexico. Modified from Rzedowski (1978). Used with permission of Editorial Limusa, México, D.F.

prominent component of shrubs with spines; a woodland is a more open community in which the crowns of the trees and shrubs do not touch; and a savanna has widely scattered trees with an understory of grasses and/or other herbaceous plants (I: pp. 20–22). In Baja California, the associations are mostly shrublands and woodlands (bosque tropical caducifolio, fide Rzedowski, 1978; Sierra de la Giganta and arid tropical region, Wiggins, 1980; seasonally dry tropical forests, Bullock et al., 1995; Gentry, 1995). In a seasonally dry tropical forest, MAP is generally below 1600 mm, and there is a long and severe dry season with five to six months with rainfall less than 100 mm. Prominent components of the shrublands and woodlands are the piñon pines *Pinus cembroides*, *P. edulis*, *P. monophylla*, and *P. quadrifolia*; the legumes *Acacia brandegeana*, *A. peninsularis*, *Cassia confinis*, *C. goldmanii*, *Cercidium microphyllum*, *Enterolobium cyclocarpum*, *Lysiloma candidum*, *L. divaricata*, *Pithecellobium confine*, *P. undulatum*, and *Prosopis glandulosa* (mesquite); the cacti *Lemaireocereus thurberi*, *Mammillaria* sp., and *Opuntia* sp.; the fan palm *Erythea brandegeei*; and *Coulterella capitata*, *Cyrtocarpa edulis*, and *Sapindus saponaria*.

There are no extensive natural grasslands in Baja California, and other communities occupy scattered areas too small to map on the scale used in Fig. 3.2. These include mangrove swamps (*Avicennia germinans* [black mangrove], *Rhizophora mangle* [red mangrove; see Fig. 3.18]); beach/strand/dune vegetation (*Ipomoea*, *Sesuvium*; see Fig. 3.23); and freshwater (*Azolla*, *Lemna*, *Potamogeton*, *Scirpus*, *Typha* [cattail], *Utricularia*) and saltwater marshes (*Salicornia bigelovii*, *Suaeda californica*).

There are coniferous forests of *Pinus* and *Quercus* (bosque de pino y encino; bosque de coniferas y de *Quercus* fide Rzedowski, 1978) at the higher elevations of the Sierra de San Pedro Mártir and the Sierra de la Giganta. The pines are *Pinus jeffreyi*, *P. lambertiana*, *P. murrayana*, and *P. quadrifolia*, along with *Abies concolor* (fir) and *Libocedrus decurrens* (incense cedar). The oaks are *Quercus brandegei*, *Q. devia*, and *Q. peninsularis*. *Alnus* (alder), *Populus* (cottonwood, poplar), and *Salix* (willow) grow along streams.

A plant that gives a distinctive character to the landscape of Baja California is the boojum (*Idria columnaris*, family Fouquieriaceae; Humphrey, 1935, 1974; Fig. 3.3). It is related to the ocotillo (*Fouquieria splendens*), a smaller version of the boojum that is also found in the Sonoran Desert; the two are possibly congeneric (Henrickson, 1972). *Idria* is restricted to central Baja California and a small area along coastal Sonora in mainland Mexico. The vernacular name was first applied by Godfrey Sykes in 1922 from a reference in Lewis Carroll's "The Hunting of the Snark," to a boojum—a strange mythical thing found in exotic regions (Humphrey, 1974). The plant was called cirio ("taper" or "candle") by the early Jesuits, and that is the name used in Mexico. Although the plant is columnar, it

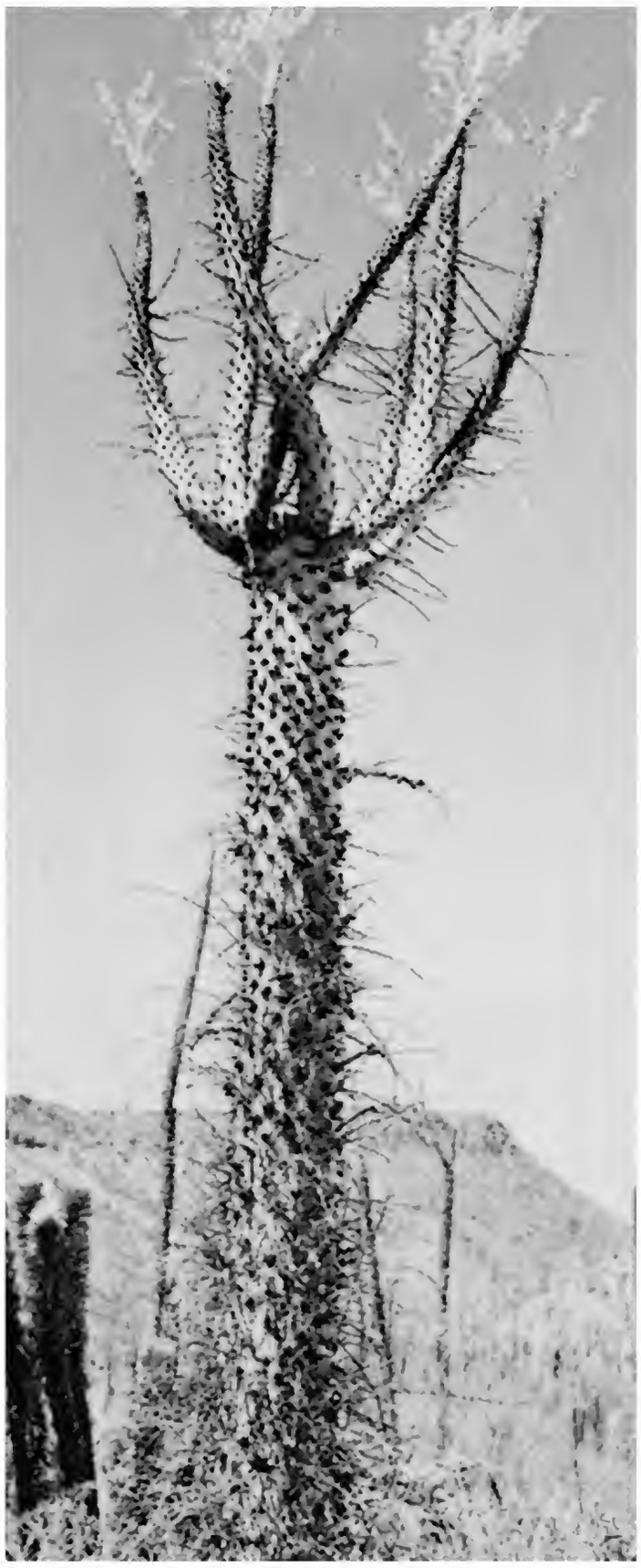


Figure 3.3. *Idria columnaris* (boojum), Baja California, Mexico. Atypical branching is due to damage of the stem apex. From Humphrey (1974). Used with permission of the University of Arizona Press, Tucson.

grows in a wide variety of bizarre shapes and reaches a maximum height of 24 m (76 ft).

The state of Baja California is separated from adjacent mainland Mexico by the Sea of Cortez (Case & Cody, 1983), but there are no significant topographic barriers and the vegetation is similar. The Sonoran Desert occupies ~126,256 km^2 (48,560 mi^2), and the climate is equally hot and dry (Table 1.2; Guaymas). MAP ranges from a minimum of 0–23 mm to a maximum of ~700 mm. In the driest parts, *Larrea tridentata* is again prominent and is associated with *Ephedra nevadensis* (Mormon tea), *Acacia cymbispina*, *Agave falcata*, *A. lecheguilla*, *Ambrosia deltoidea* (bursage), *Bursera microphylla*, the cacti *Echinocactus*, *Echinocereus*, *Mammillaria*, and *Opuntia imbricata*, *Cercidium microphyllum* (palo verde), *Encelia farinosa* (brittlebush), *Euphorbia antisyphilitica*, *Flourensia cernua*, *Fouquieria splendens* (ocotillo), *Hechtia*, *Olneya tesota* (ironwood), *Parkinsonia aculeata*, *Prosopis juliflora*, *Yucca australis*, *Y. carnerosana*, *Y. elata*, *Y. macrocarpa*, and *Y. treculeana* (Shreve, in Shreve & Wiggins, 1964; Wiggins, 1980; Delgadillo, 1992).

In contrast, the Sierra Madre Occidental does form a topographic barrier between the Sonoran Desert of Baja California–northwestern Mexico and the Chihuahuan Desert of northeastern Mexico (Figs. 3.4, 3.5; Muldavin, 2002). The latter occupies 453,000 km^2, has less rainfall (150–400 mm; avg. 235 mm), is mostly higher (1100–1500 m up to 2000 m in the south), and is cooler (14°–23° C; avg. 18.6° C) (Hendrikson & Straw, 1976; Medellín-Lean, 1982; Hendrikson & Johnston, 1986; MacMahon, 2000). *Larrea tridentata* (Figs. 3.5, 3.6) is prominent, along with *Acacia neovernicosa*, *Agave lecheguilla*, the grass *Bouteloua eriopoda*, the cacti *Ferocactus latispinus* and *Myrtillocactus geometrizans* (Figs. 3.7, 3.8), *Dalea formosa*, *Dasylirion leiophyllum* (sotol), *Flourensia cernua*, *Fouquieria splendens*, *Jatropha dioica*, *Koeberlinia spinosa*, *Leucophyllum frutescens* (purple sage), *Parthenium argentatum*, *P. incanum*, *Yucca carnerosana*, *Y. elata*, *Y. filifera*, *Y. thompsoniana*, and *Y. torreyi*.

The most conspicuous controls on the distribution of *Larrea tridentata* within the dry regions of Mexico are moisture, slope, and soil. Near the base of mountains where moisture from runoff is greatest, the vegetation is a slightly more mesic shrubland, whereas farther out on the driest flatlands, creosote bush becomes the dominant plant. However, the local geology also plays a role. Laguna El Fresnal, in the Chihuahuan Desert southwest of El Paso–Ciudad Juárez, is a fault-bounded depression in the Basin and Range Province of the Río Grande Rift. The western slope is characterized by relatively well-consolidated alluvial fans, debris flows, braided stream deposits, and sheet flood deposits, in contrast to the eastern slope composed of unconsolidated aeolian (wind-deposited) sediments blown in from the west (Campos-Enriquez et al., 1999). The water-holding capacity of the eastern deposits is less than those to the west, reflecting the different sediment types, and the result is shrubland to the west (*Juniperus*, *Prosopis*) and creosote bush to the east within a zone of identical rainfall.

Many of the same plants are found in the Sonoran and Chihuahuan deserts, but one noticeable difference is that the former has more tall columnar cacti (*Carnegiea gigantea*, saguaro, I: fig. 1.14; *Lemaireocereus thurberi*, organ pipe cactus). Although this growth form does occur in the Chihuahuan Desert (e.g., *Cephalocereus*; *Myrtillocactus geometrizans*, Figs. 3.7, 3.8; *Pachycereus*, Fig. 3.7), that desert is characterized more by pad and candelabra (cholla-type) *Opuntia*, and smaller cacti such as *Echinocereus* ('tricolor,' rainbow cactus), *Lophophora williamsii* (peyote; Fig. 3.9), and others. Columnar forms become more abundant toward San Luis Potosí (Fig. 3.7), and farther south they give a distinctive aspect to the landscape along Mexico Highway 131 through the Tehuacán Valley (*Neobuxbaumia tetetzo*; Fig. 3.10), together with *Beaucarnea gracilis* and the large barrel cactus *Echinocactus grandis*.

In dry environments, opportunities for the preservation of

Figure 3.4. Chihuahuan Desert, San Luis Potosí, Mexico. The near-spineless cactus is *Opuntia microdasys*, and the small shrub is a species of *Mimosa*.

megafossils (leaves, flowers, fruits, seeds) are limited. Two exceptions are petrified wood (e.g., Schulman, 1956; I: pp. 128–131), and plant debris incorporated into the middens (nests) of the pack rat *Neotoma* and preserved in protected rock shelters (Betancourt, 2004; Betancourt et al., 1990; I: pp. 131–137). Analysis of pack rat middens has been used extensively for Quaternary paleoenvironmental reconstructions in the Sonoran and Chihuahuan deserts of the southwestern United States and Mexico, and studies are under way in the Atacama Desert of Chile. Plant microfossils (pollen, spores, phytoliths [Piperno, 1988], diatoms, and other algae) preserve in playa lake and basin sediments (e.g., the Cuatro Ciénegas Basin of Coahuila), and they may be recovered from near-shore marine deposits (e.g., the Gulf of California). In general, however, the pollen occurs in low concentrations and does not preserve well at the high pH typical of alkaline desert deposits. As such, the sources of error common to all microfossil assemblages loom even larger for these deposits. There are no spore and pollen catalogs available for the desert regions of Mexico, but Hendrickson (1973) describes the pollen of modern Fouquieriaceae, and the pollen of other genera that grow in the southern United States but also extend into Mexico are illustrated by Jones et al. (1995; e.g., *Yucca*, *Acacia*, chenoams, *Dalea*, *Leucophyllum*, *Opuntia*, *Prosopis*, and *Sapindus*; see also Figs. 3.56, 3.57).

Even where plant microfossils are available, the reconstruction of desert vegetation and the tracing of its geologic history are complicated by the pollen signature of the community (Lozano-García, 1984). Several important members of the desert and other communities of arid habitats produce generalized pollen types that are difficult to identify as isolated microfossils using the magnifications of the light microscope. Probable identifications are possible from late Quaternary sediments where choices likely can be limited to plants still growing in the region. These include the small microreticulate grains of

Figure 3.5. Chihuahuan Desert, San Luis Potosí, Mexico. The tall columnar plant is *Yucca carnerosana*, with the shrub *Larrea tridentata* (creosote bush) and the cactus *Opuntia* sp.

Figure 3.6. *Larrea tridentata.* This shrub occupies the driest regions of the Sonoran Desert of Baja California and northwestern Mexico, and the Chihuahuan Desert of northeastern Mexico. It typically grows on flats beyond the base of mountain slopes that receive moisture from runoff.

Larrea, the larger reticulate grains of *Cercidium*, the more distinctly reticulate grains of *Fouquieria*, and the faintly scabrate grains of *Prosopis*. Others are more easily recognized, such as the polyads of *Acacia*, the echinate grains of *Ambrosia* that are also vesiculate (viz., with air sacs separating the layers of the pollen wall), and the small striate pollen of *Bursera*. All of these have been reported from the Cenozoic of Mexico.

A further difficulty, however, is that many of the genera also occur within or marginal to other vegetation types in open or disturbed habitats, and their presence in fossil assemblages cannot be assumed a priori to indicate extensive dry to arid vegetation. For example, pollen of *Ambrosia* is known from the fossil record of Mexico, and while *A. deltoidea* is the burrsage of the Sonoran Desert, *A. trifida* and related species of ragweed with similar pollen grow in a wide variety of habitats. There are other limitations to the use of plant microfossils in reconstructing dry habitat vegetation. The Cactaceae are an important family of the New World deserts, but they are insect pollinated, producing small amounts of large, sticky pollen. Genera of the Chenopodiaceae (e.g., *Atriplex*, *Salicornia*, *Suaeda*) and Amaranthaceae (*Amaranthus*) are wind pollinated, producing copious amounts of pollen well-represented in late Cenozoic deposits, but the pollen is mostly similar in both families and is identified in the paleopalynological literature as "chenoams." It probably would be possible to detect the desert plant formation in microfossil floras if the proper combina-

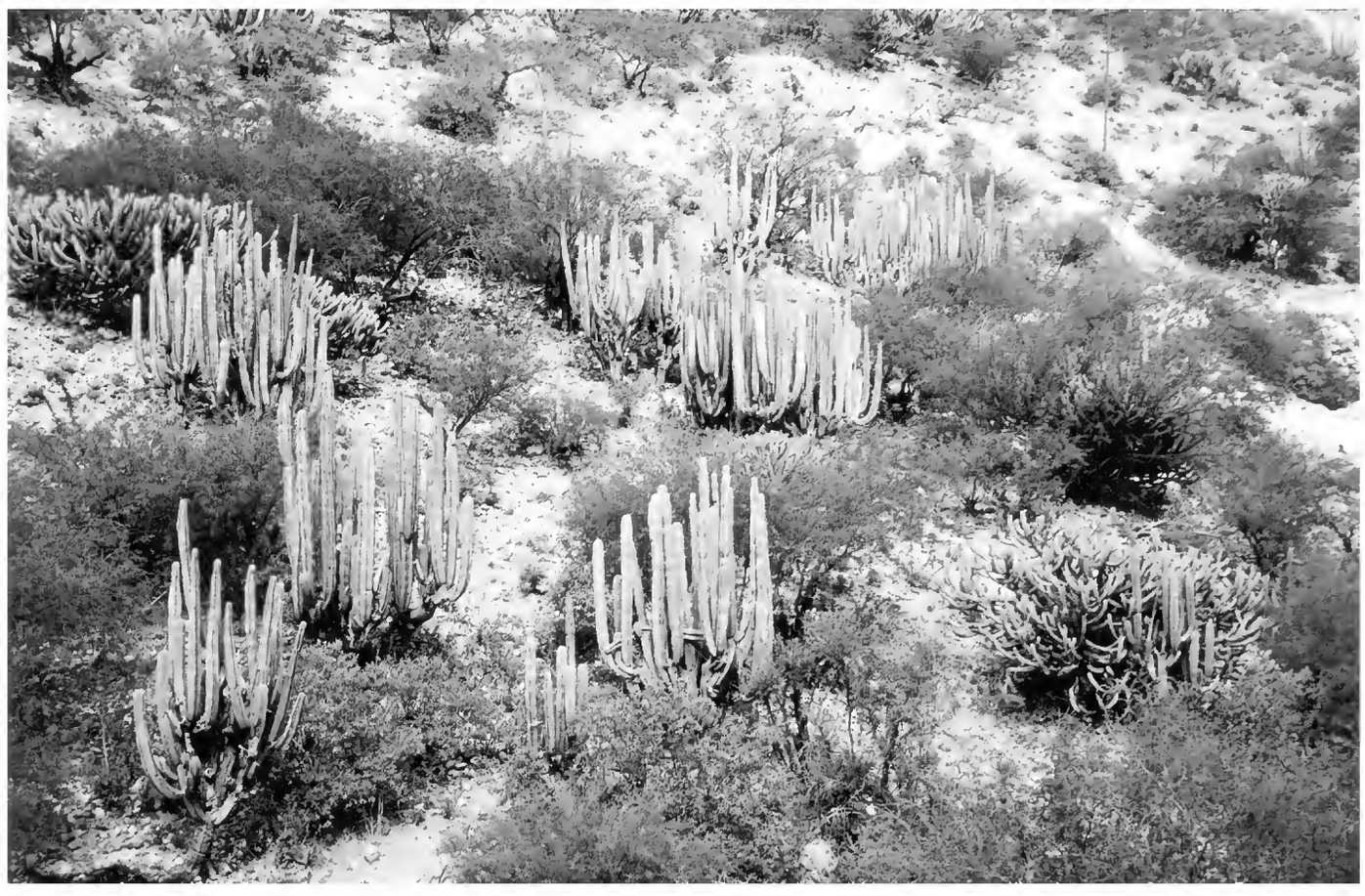


Figure 3.7. Desert vegetation in the state of San Luis Potosí, Mexico. The prominent cacti are *Pachycereus* (tall columnar) and *Myrtillocactus* (lower branched).

tion of distinctive taxa were the only requirement. However, during the Late Cretaceous through about the early Miocene, tropical and mesic environments were prevalent, while dry to arid vegetation was limited. Instead, individual elements occupied restricted habitats created by slope, wind, exposure, and edaphic conditions and grew intermingled with more prominent mesic vegetation. These preadapted elements coalesced with the onset of drying conditions later in the early middle Miocene, with the uplift of the Sierra Madre Occidental and Oriental to rain shadow heights in the Pliocene, and during the climatically turbulent climates of the Quaternary (I: ch. 7, 8). Thus, in addition to spores, pollen, diatoms, and phytoliths, the history of desert vegetation must be reconstructed from multiple sources of information (e.g., rodent middens) and disentangled from that of other communities. This is difficult based on the limited plant fossils alone, but dry environments can be anticipated from orogenic histories and global climate trends and inferred from sediment types (e.g., red beds, evaporates such as gypsum and salt, layering in stalactites). A general history of desert vegetation is available utilizing this context information. These sources and this history are presented in Chapter 4.

Figure 3.8. Stems and edible fruits of *Myrtillocactus geometrizans.*

Shrubland/chaparral–woodland–savanna (bosque tropical caducifolio, tropical deciduous woods; bosque tropical subcaducifolio, seasonally dry tropical forests; bosque espinosa [chaparral]; savanna)—Dry areas of mainland Mexico receiving slightly more moisture than the desert support a vegetation of low shrubs from 4–15 m tall. Shrubland occurs on the lower west-facing slopes of the Sierra Madre Occidental, south of the Transvolcanic Belt along the Balsas Depression, in the southern part of the Isthmus of Tehuantepec (Fig. 3.11), in the vicinity of the Sierra Madre de Chiapas (Central Depression), along the Veracruz coast, and in the northern Yucatán Peninsula (e.g., in the Helen Moyers Biocultural Reserve at Rancho Kiuic, central Yucatán). It covers ~8% of the landscape of Mexico at elevations mostly between sea level and 1900 m. The MAT is typically between 20° and 29° C. The characteristic feature of this community is that although there is more total moisture (~1000 mm) than in the desert, precipitation is distinctly seasonal and the trees are deciduous during the pronounced dry season. Prominent members are the cultivated *Agave fourcroydes* (henequen), *Bursera aptera*, *B. copallifera*, *B. longipes*, *B. morelensis*, *Ceiba aesculifolia*, *Comocladia engleriana*, *Cyrtocarpa procera*, *Euphorbia schlechtendalii*, *Haematoxylum brasiletto*, *Karwinskia humboldtiana*, *Lippia graveolens*, *Lysiloma tergeminum*, *Neobuxbaumia mezcalaensis*, *Rhus pachyrrhachis*, and *Zanthoxylum liebmannianum*.

Where the community includes a prominent spiny compo-

Figure 3.9. *Lophophora williamsii* (peyote), Nuevo León, Mexico.

Figure 3.10. *Neobuxbaumia tetetzo*, Tehuacán Valley, Puebla, Mexico.

Figure 3.11. Shrubland/chaparral–woodland–savanna (bosque tropical caducifolio; seasonally dry tropical forest) with *Juliania adstringens* (cuachalala) near Tehuantepec, Isthmus of Tehuantepec, Mexico. The photograph by A. Maya was taken in May of the dry season. From Wagner (1964).

Figure 3.12. Savanna of *Curatella americana*, south of Tuxtla Gutiérrez, Chiapas, Mexico, elevation 550 m. From Wagner (1964). Photograph by Faustino Miranda.

Figure 3.13. Palm stand (palmar) of *Sabal mexicana*, Veracruz, Mexico. In drier habitats, *Sabal* may form a savanna-like communitity but one likely resulting from human activity.

nent, it is called chaparral (bosque espinosa), and this vegetation type constitutes ~5% of the vegetation of Mexico. It is often found on flat surfaces to the lee of mountains or peninsulas such as on the coastal mainland side of the Gulf of California, to the east of the Sierra Madre Oriental, to the south of the Transvolcanic Belt, and in smaller areas west of the Sierra Madre del Sur, along the Pacific Coastal Plain of the Isthmus of Tehuantepec, and on the east-facing Caribbean side of the Yucatán Peninsula. It occupies low to middle elevations to a maximum of ~2000 m.

In northwestern Mexico, prominent members are *Acacia greggii*, *Bursera laxiflora*, *B. microphylla*, *Caesalpinia pumila*, *Cercidium floridum*, *Fouquieria macdougalii*, *Jatropha cordata*, *Lysiloma divaricata*, *Mimosa* sp., *Piscidia mollis*, *Prosopis velutina*, and others. In the Valle del Río Mayo (Gentry, 1942), many of the same genera and some species are found (*Acacia*, *Bursera*, *Cercidium*, *Fouquieria*, *Jatropha*, *Mimosa*, *Prosopis*). In other areas to the south, *Haematoxylum brasiletto*, *Ipomoea arborescens* (tree morning glory), *Juliania adstringens* (cuachalala; Fig. 3.11), and *Pithecellobium tortum* appear or become more prominent. Chaparral extends through a wide range of climates, but typical MATs are 17°–29° C and MAP varies from 350–1200 mm with a dry season of five to six months (Rzedowski, 1978). Regions with higher rainfall, as along the coastal Yucatán Peninsula, support similar vegetation but on coarser, more porous soils.

Woodlands (bosque tropical subcaducifoio [tropical semideciduous forest]; seasonally dry tropical forest) occur in regions with slightly greater precipitation, at the base of slopes,

Figure 3.14. Palm stand (palmar) of *Orbignya cohune*, near Manzanillo, Colima, Mexico.

Figure 3.15. Low deciduous selva (selva baja caducifolio), with *Brahea dulcis* (Arecaceae), near Tehuacán, Puebla, Mexico.

on soils with greater water-holding capacity or higher water tables, and in areas receiving moisture from the ocean. They are usually semi-deciduous; that is, not all the trees lose their leaves during the same part of the dry season. This community is found mostly along the Pacific coast of central and southern Mexico and at a few sites on the Atlantic side, such as a small area between Matamoros and Tampico, and across the central Yucatán Peninsula. It covers ~4% of the landscape of Mexico, mostly between sea level and 1300 m. The MAT ranges between 20° and 28° C and the MAP is 1000–1600 mm. Members include *Astronium graveolens*, *Brosimum alicastrum*, *Cedrela mexicana* (Mexican mahogany), *Celtis monoica* (hackberry), *Dalbergia granadillo*, *Enterolobium cyclocarpum*, *Erythroxylum deciduum*, *Hymenaea courbaril*, *Platymiscium dimorphandrum*, *Roseodendron donnell-smithii*, and *Vitex gaumeri*.

Savannas in Mexico have scattered trees mostly of *Byrsonima crassifolia*, *Crescentia cujete*, *Curatella americana* (Fig. 3.12), and/or *Paurotis wrightii*. The latter is a palm, and palm savannas (palmar) as a plant formation, as well as palm stands as associations or phases, are likely anthropogenic and owe their present extent, if not their origin, to planting and selective cutting because of the economic importance of the plants (Figs. 3.13, 3.14). There is no evidence in the fossil record of Mexico of a natural plant formation dominated by palms.

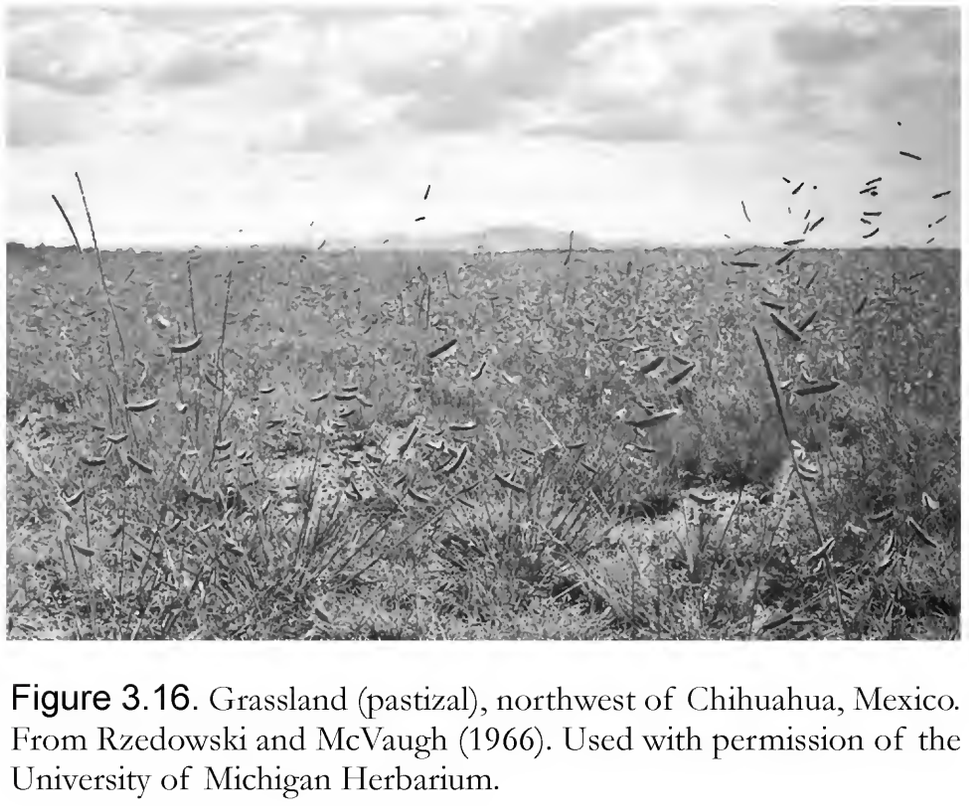


Figure 3.16. Grassland (pastizal), northwest of Chihuahua, Mexico. From Rzedowski and McVaugh (1966). Used with permission of the University of Michigan Herbarium.

As noted previously, it is difficult to distinguish between the several shrublands, woodlands (bosques), and low forests (selvas; Fig. 3.15), even in the modern vegetation, and especially in fossil assemblages. Thus, they have been grouped here under shrubland/chaparral–woodland–savanna and include essentially the dry woody communities of Mexico slightly more mesic than the desert and drier than the forests.

Leaves and other megascopic remains of this complex have not been reported directly from the Tertiary fossil record of Mexico, but some are preserved in the late Miocene Mint Canyon flora presently of southern California and transported from coastal Sonora by plate movement. Other megafossils are known from packrat middens of Quaternary age (Chapter 4), and additional information comes from the study of petrified wood. The pollen signatures of shrublands, chaparral, woodlands, savanna, and dry selvas overlap and, like deserts, the taphonomy (preservation process) is biased against their preservation. Thus, it is rare that these dry-habitat associations are ever found extensively represented as distinct and easily recognizable communities in the pre-Late Glacial fossil record. Pollen from the shrubland/chaparral–woodland–savanna and dry selvas blow into lowland basins of deposition or are preened from pack rats into midden debris. Evidence for the community must be disentangled from assemblages that include elements from the surrounding vegetation. This tedious task requires extensive reference collections based on vouchered and well-identified herbarium material, and the motivation to establish the biological affinities of the specimens. Among the modern genera mentioned, *Acacia*, *Bursera*, *Caesalpinia*, *Ce-*

Figure 3.17. Grassland (zacatonal) of *Bouteloua gracilis*, Jalisco, Mexico.

drela, *Celtis*, *Comocladia*, and *Mimosa* have been reported from the Cenozoic of Mexico. Innovative approaches may gradually add to the list of fossil plants from dry tropical regions. For example, chemical analysis of an Oligo–Miocene amber in Chiapas revealed that the amber was produced by *Hymenaea* (Leguminosae). Thus, the genus may be added to the inventory of fossil plants from the region even when traditional fossils are not found.

Grassland (pastizal, zacatonal)—Pastizal (Fig. 3.16) is the dry grassland of mid-elevations in northern and central Mexico, and zacatonal (Fig. 3.17) is the mesic grasslands of higher elevations. Several environmental conditions combine in Mexico to support communities in which the Poaceae (grasses) are prominent. The Sierra Madre Occidental blocks rain coming off the Pacific Ocean, but runoff provides some moisture on the leeward side. The precipitation is too low to support forests, but it is higher than in deserts, and this is one factor in producing an environment favorable to the growth of grasses. Calcareous soils resulting from the limestone bedrock of the Altiplanicie is another factor, and upland temperatures that are cooler than in the desert reduce the evapotranspiration potential. Fire and grazing maintains and overgrazing has expanded grasslands, especially in northern Mexico. Where these conditions prevail at the interface with forests, there is often savanna. In the classification of Rzedowski (1978), pastizal also includes savanna, as well as desert grassland with intervening bare soil between bunch grasses such as *Bouteloua chasei* and *Muhlenbergia purpusii*, and alpine tundra (páramo) on the volcanoes of the Transvolcanic Belt. Pastizal constitutes 10%–12% of the vegetation cover of Mexico.

Grasslands have a considerable altitudinal range in Mexico, they form a transition with other vegetation types (desert,

Figure 3.18. Mangrove (manglar) of *Rhizophora mangle* (red mangrove) along bay near UNAM's tropical biological station, Catemaco, Veracruz, Mexico.

Figure 3.19. Leaf and flower of *Hibiscus tiliaceus*. From TROPICOS, photograph by Alwyn Gentry. Used with permission of the Missouri Botanical Garden, St. Louis.

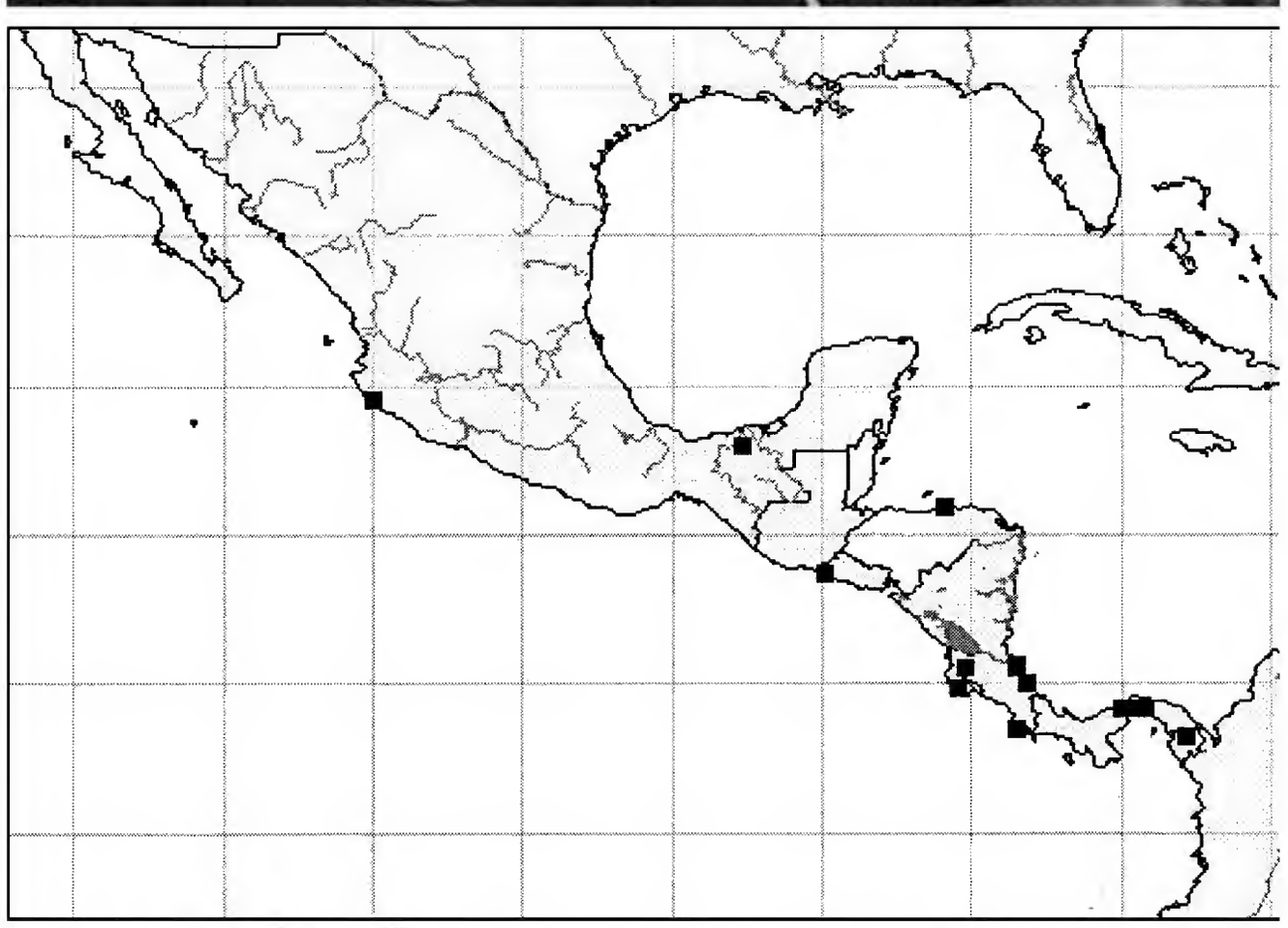


Figure 3.20. Mesoamerican distribution of *Hibiscus tiliaceus* from collections presently mapped. From TROPICOS. Used with permission of the Missouri Botanical Garden, St. Louis.

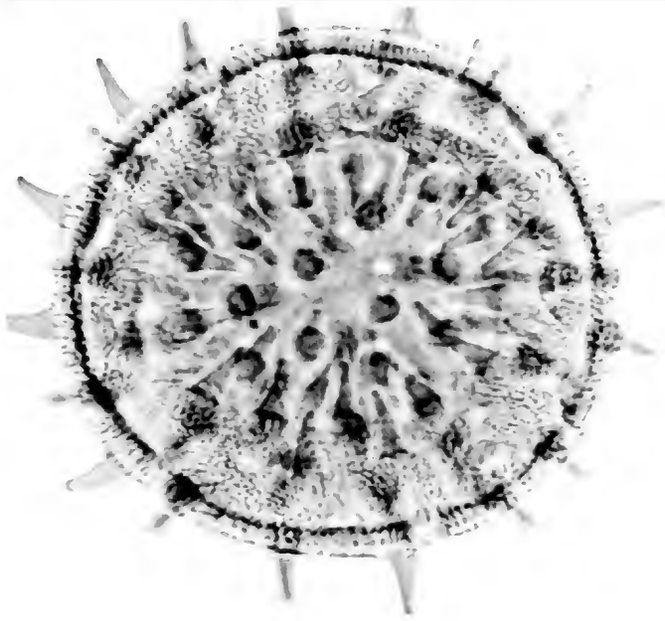


Figure 3.21 (left). Modern pollen of *Hibiscus militaris*.

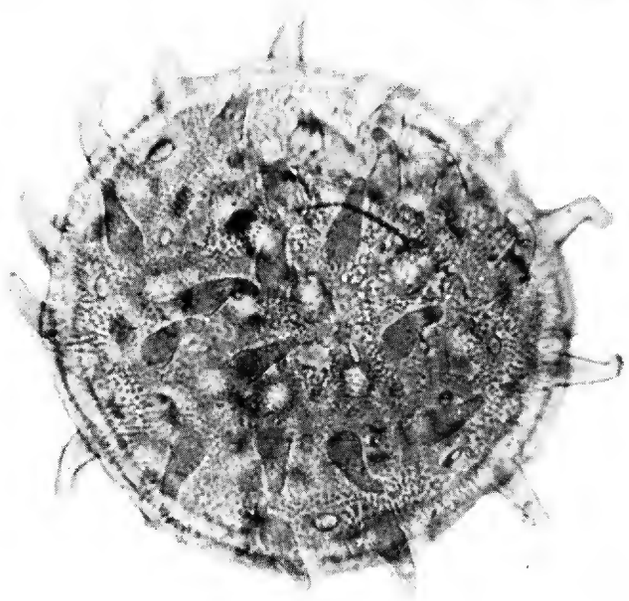


Figure 3.22 (right). Fossil pollen of *Hampea*/*Hibiscus* from the middle Pliocene Parajé Solo Formation, Veracruz, Mexico.

savanna), and their range is partly anthropogenic. Throughout their greatest extent along the eastern slopes of the Sierra Madre Occidental, the altitudinal range is 1100–2500 m, the MAT 12°–20° C, and the MAP is 300–600 mm with a dry season of six months to as many as nine months in the driest parts. In the high elevations to the south, MAT may be as low as 3°–5° C, with extremes to –10° C, and MAP as high as 800 mm.

An extensive list of grasses from the pastizal and zacotonal is not germane to a discussion of vegetation history because remains of the family are not extensive in fossil floras. Leaf fragments are mostly unidentifiable to the generic level, and the Poaceae are distinctly stenopalynous; that is, virtually no genera can be distinguished on the basis of pollen characters (see Fig. 3.56e; Geisler, 1945). An exception, fortunate for palynological-archeological studies, is *Zea mays* (maize, corn), which has pollen 80–100 μm in diameter compared to an average of 30–35 μm for other genera. Another is *Pariana*, a primitive genus of 21 species of tropical bamboo grasses, which is distinctive in lacking an annulus around the pore (Skvarla et al., 2003). Achenes (I: ch. 7, pp. 250–251) and some phytoliths can be identified to genus, but few remains have been reported from the Tertiary of Mexico, and they are not extensive in the Quaternary. However, the ability to detect shifts even between forest and grassland, be it on the basis of pollen, achenes, phytoliths, or cuticles, is important for paleovegetation and faunal studies and for placing events in human history in an environmental context. Among the principal genera of grasses in Mexico are *Andropogon*, *Aristida*, *Bouteloua*, *Bromus*, *Buchloe*, *Eragrostis*, *Hilaria*, *Muhlenbergia*, *Setaria*, *Sporobolus*, and *Stipa*.

Figure 3.23. Beach/strand/dune plant formation, Laguna Madre, Brownsville (Texas)–Matamoros (Mexico). The grass is *Uniola paniculata*, and the vines are *Ipomoea pes-caprae* and *I. stolonifera*.

Mangrove (included under vegetación acuática y subacuática in Rzedowski, 1978; manglar)—Mangrove is a plant formation of dense shrubs with distinctive prop roots growing along coasts, bays, and estuaries where rivers empty into the ocean creating brackish-water conditions (Davis, 1940; Reimold & Queen, 1974; Tomlinson, 1986; Hutchings & Saenger, 1987; Hogarth, 1999; Seeliger, 1992). They also grow inland along the lower reaches of rivers influenced by saline waters at high tide. There is usually a zonation in mangrove vegetation reflecting the degree of tolerance to salt water and to disturbance from the shifting substrate (e.g., López-Portillo & Ezcurra, 1989). The outer zone is typically occupied by *Rhizophora mangle* (red mangrove; Fig. 3.18), and inland by *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), and/or *Conocarpus erectus* (buttonwood). Other plants found in or marginal to the mangroves include the fern *Acrostichum aureum*, *Hibiscus tiliaceus* (Figs. 3.19–3.22), and *Pterocarpus officinalis*. In Mexico, mangroves occur along the Pacific coast south of Mazatlán and along the Gulf of Mexico in Veracruz, Tabasco, Campeche, and the northern Yucatán Peninsula.

Mangroves and the mangrove environment are important for the study of tropical vegetation history. Paleoecologically, they indicate (1) lowland coastal habitats, and (2) tropical to subtropical climates where minimum cold-month tempera-

Figure 3.24. Broad-leaved marsh of *Thalia geniculata* (popal) near the Río Coatzacoalcos, Veracruz, Mexico.

Figure 3.25. *Thalia geniculata* near the Río Coatzacoalcos, Veracruz, Mexico.

Figure 3.26. Lowland tropical rain forest, karst substrate, Uxpanapa, Veracruz, Mexico, with *Poulsenia armata* (left). Photograph by Tom Wendt.

tures are mostly above 0° C because the plants cannot tolerate significant or prolonged freezing. The dense prop roots slow the removal of organic matter by offshore currents, and the rivers provide abundant fine-grained material for the rapid accumulation of sediments. Decay of the abundant plant and animal remains and the stagnant, poorly aerated, acid waters reduce microbial activity, further facilitating the preservation of plant microfossils. As a result, there are numerous localities in Mexico and elsewhere in Latin America where lignites alternate with repeating sequences of clay and siltstones rich in plant microfossils. A 10-gram sample of these sediments (about the size of a marble) can yield thousands of palynomorphs, sometimes dominated by *Rhizophora* (>95%), but often containing 200 or more other spore and pollen types. This provides an extensive inventory of plants growing in the vicinity at the time of deposition. *Acrostichum* type, *Hibiscus*, *Laguncularia*, and *Rhizophora* have all been reported from the Cenozoic of Mexico, and the initial appearance, spread, and diversification of mangroves is one of the best documented of the tropical plant formations (Chapter 8).

Beach/strand/dune—Throughout the Gulf–Caribbean region and in other parts of the world, there are plants adapted to the haline, desiccating, and unconsolidated substrates and strong winds of the beach environment (Fig. 3.23). Among these are the scandent morning glory vines *Ipomoea pes-caprae* and *I. stolonifera*; the succulent *Sesuvium portulacastrum*; the fibrous-rooted grass *Uniola paniculata* (sea oats); the low shrubs *Batis maritima*, *Canavalia maritima*, and *Coccoloba uvifera*; the chenoam *Iresine*; and others that extend into this community from different habitats (*Acacia*, *Caesalpinia*, *Casearia*, *Laguncularia*, *Terminalia*, *Tournefortia*). Gómez-Pompa (1973, p. 143) lists other members of this plant formation that grow along the coast of Veracruz and on Isla Verde offshore from the port of Veracruz.

The shifting depositional environment and the coarse sandy sediments preclude the preservation of fossils; the pollen of *Uniola paniculata* cannot be distinguished from that of non-coastal grasses; and other components are insect pollinated and unlikely to be represented (e.g., *Ipomoea*). Some pollen can be blown or washed into adjacent mangrove swamps and preserved in lignites, and *Acacia*, *Casearia*, *Coccoloba*, *Iresine*, *Laguncularia*, *Terminalia* type, and *Tournefortia* have been reported from the Cenozoic of Mexico. However, these genera range into other vegetation types, and there is limited direct evidence for tracing the history of the beach/strand/dune plant formation based only on plant fossils.

Freshwater herbaceous bog/marsh/swamp—Herbaceous broad-leaved marsh (popal) association: This is a freshwater marsh community of herbaceous plants characterized by the broad-leaved *Thalia geniculata* (Figs. 3.24, 3.25), frequently associated with *Calathea*, *Heliconia*, *Pachira*, and *Pontederia*.

Herbaceous reed-sedge marsh (tule/carrizal) association: This is a freshwater marsh of the narrow-leaved, herbaceous *Typha* (tule, cattails) and *Phragmites communis* (carrizal, reeds) and other grasses associated with Cyperaceae (sedges; e.g., *Scirpus*;

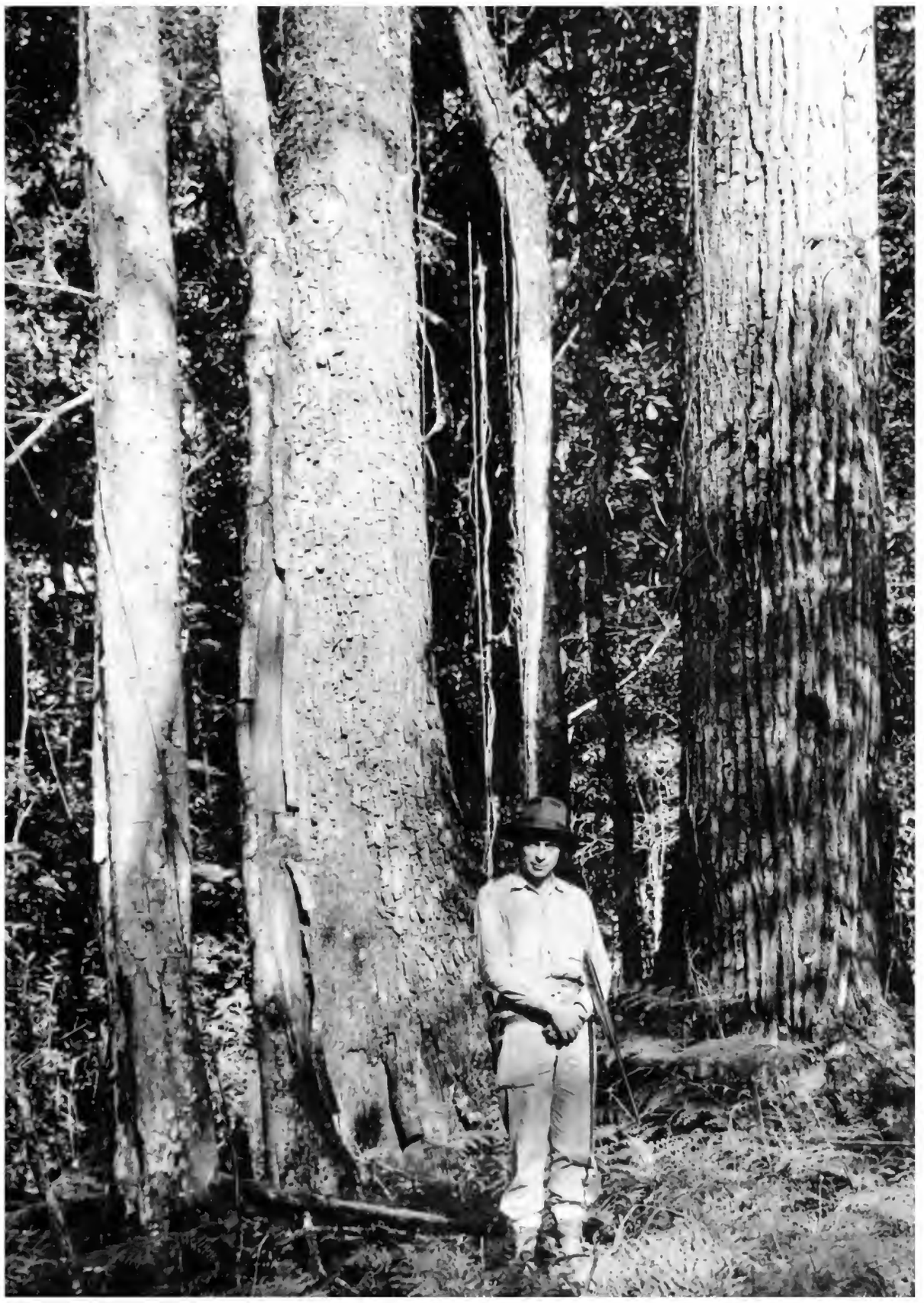


Figure 3.27. Lowland tropical rain forest/lower to upper montane broad-leaved forest transition (elevation ~500 m). The large tree on the right is *Swietenia macrophylla* (mahogany) and the one on the left is *Calophyllum brasiliense* (bari). The person in the photograph is Faustino Miranda. Lacandón region, Chiapas, Mexico. From Wagner (1964). F. Miranda photograph.

see Figs. 3.56d, 3.151, 3.152) and Juncaceae (rushes; e.g., *Juncus*).

Aquatic—Submerged or floating aquatic plants in Mexico include *Ceratopteris* and *Salvinia* (floating ferns), *Cabomba*, *Ceratophyllum*, *Eichhornia crassipes* (water hyacinth), *Lemna* (the minute duckweed), *Myriophyllum*, *Nymphoides fallax*, *Pistia stratiotes*, *Potamogeton*, *Utricularia*, and *Vallisneria*.

Lowland freshwater habitats supporting popal, tule/carrizal, and aquatic vegetation are also basins of deposition for organic and fine-grained mineral matter suitable for the preservation of spores and pollen. The sediments may be converted into lignites but, unlike those formed under brackish-water conditions, they lack abundant remains of *Rhizophora* and other mangroves. Pollen of *Ceratopteris*, Cyperaceae, Poaceae, *Typha*, *Thalia*, and *Utricularia* is known from the Cenozoic of Mexico, and *Cabomba* from the Miocene of Panama (Chapter 6).

Lowland tropical rain forest (bosque tropical perennifolio; selva alta perennifolia; Fig. 3.26; transition to lower wetter phase of the montane broad-leaved forest, Fig. 3.27)—

> "Or it could be that the irreversible degradation of the environment [will be what puts] a stop to our history, an eventuality Lucretius [d. 55 A.D.] did not anticipate, though he did describe the beginnings of the process when he spoke of metallurgy giving men 'tools to fell the forests,' and of the way humans 'forced the forests to recede up to the mountain….'" (M. Cook, 2003, *A Brief History of the Human Race*, W. W. Norton, New York)

The northernmost occurrence of lowland tropical rain forest in the New World is in Veracruz, Mexico, near latitude 18°N in the vicinity of Catemaco. A small remnant of this forest is preserved in UNAM's tropical biological station (Estación de Biología Tropical Los Tuxtlas; González Soriano et al., 1997), but land clearing has proceeded to the very fence that surrounds the station (Fig. 3.28). The composition of the tropical rain forest in Mexico is given in a later section on

Figure 3.28. Remnant of the lowland tropical rain forest at UNAM's tropical biological station at Catemaco, Veracruz, Mexico (see also I: figs. 2.25, 2.26).

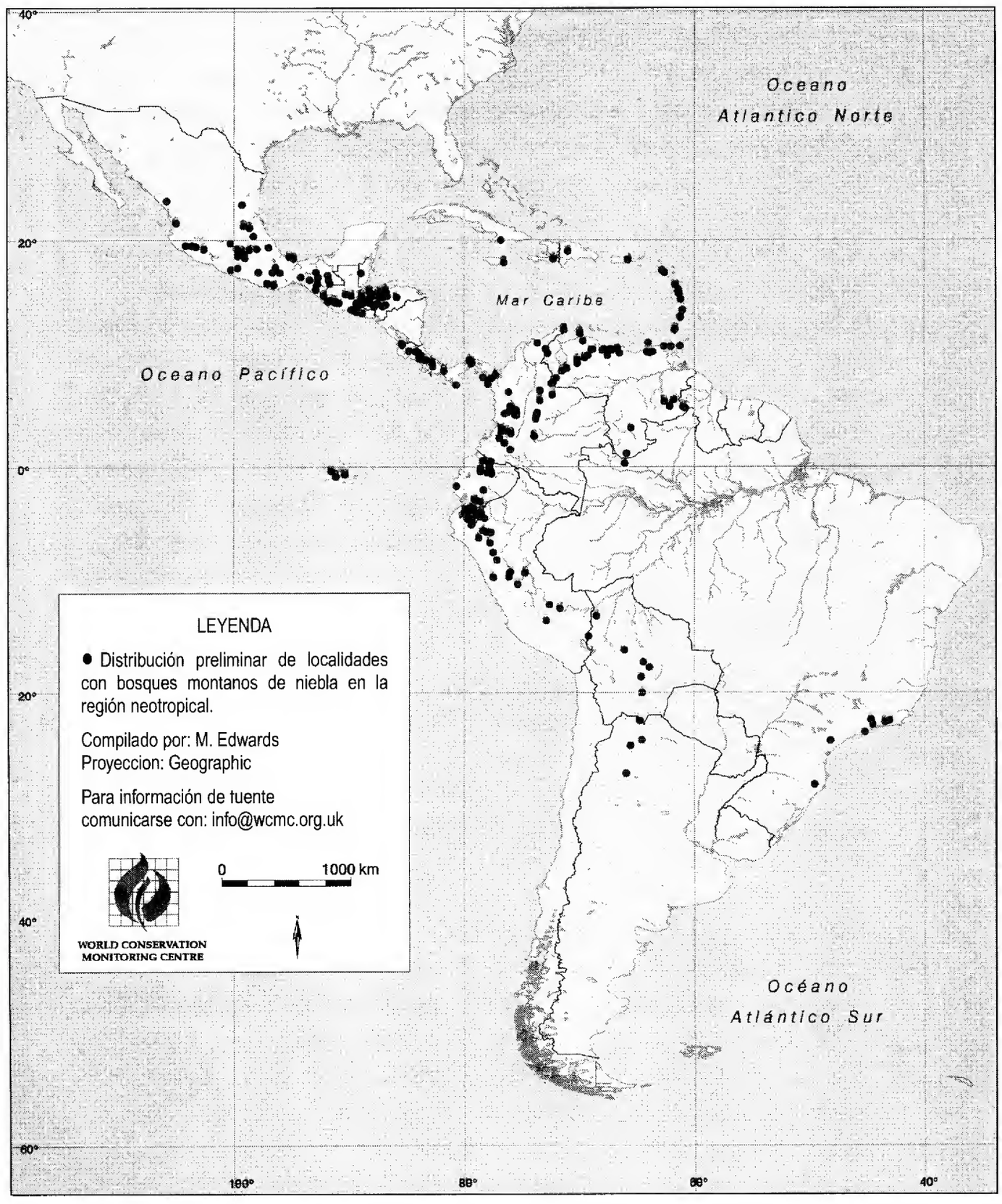


Figure 3.29. Distribution of cloud forest vegetation in the Neotropics. From Bubb (2001). Used with permission of Editorial INBio, Santo Domingo de Heredia, Costa Rica.

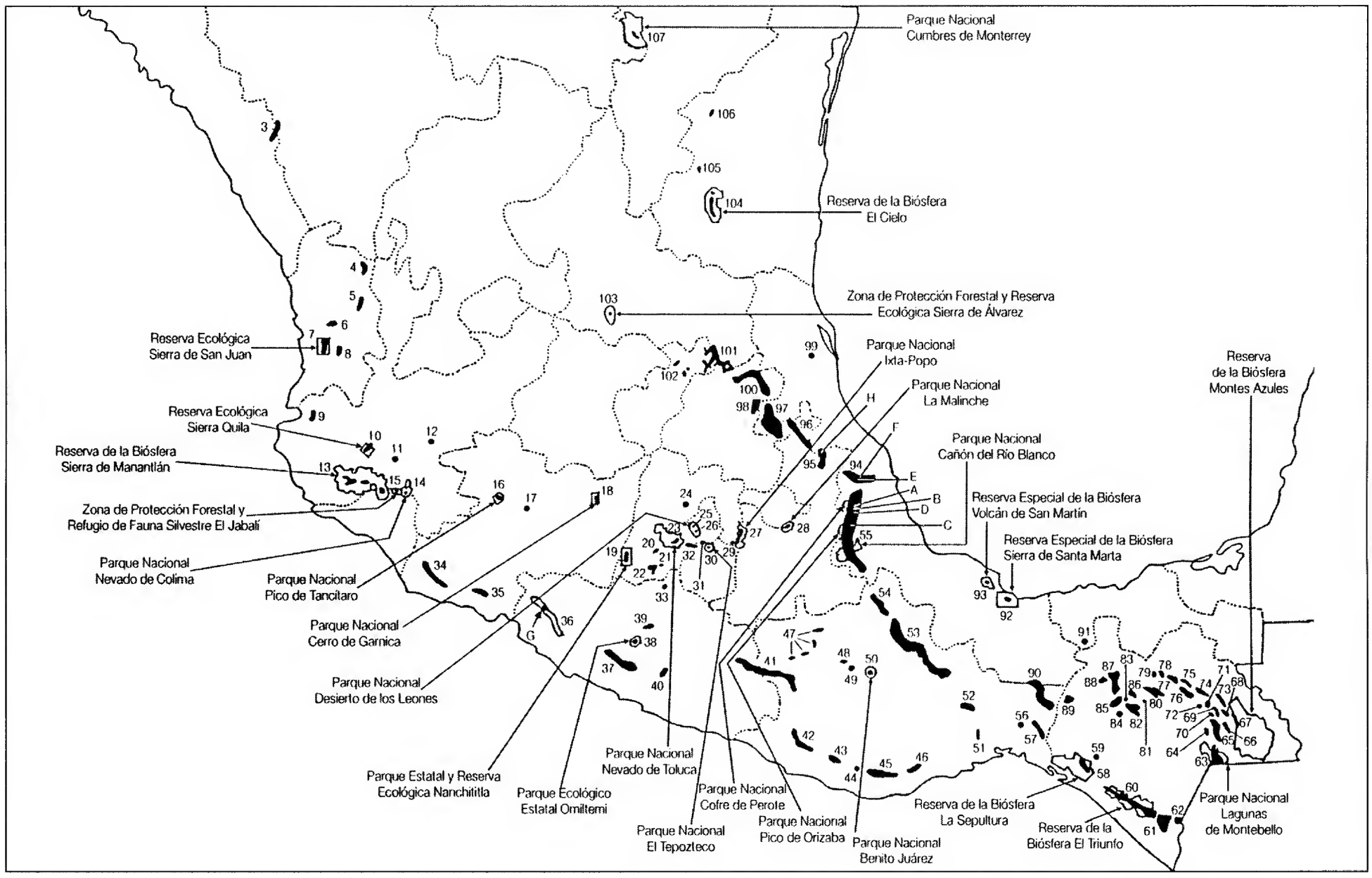
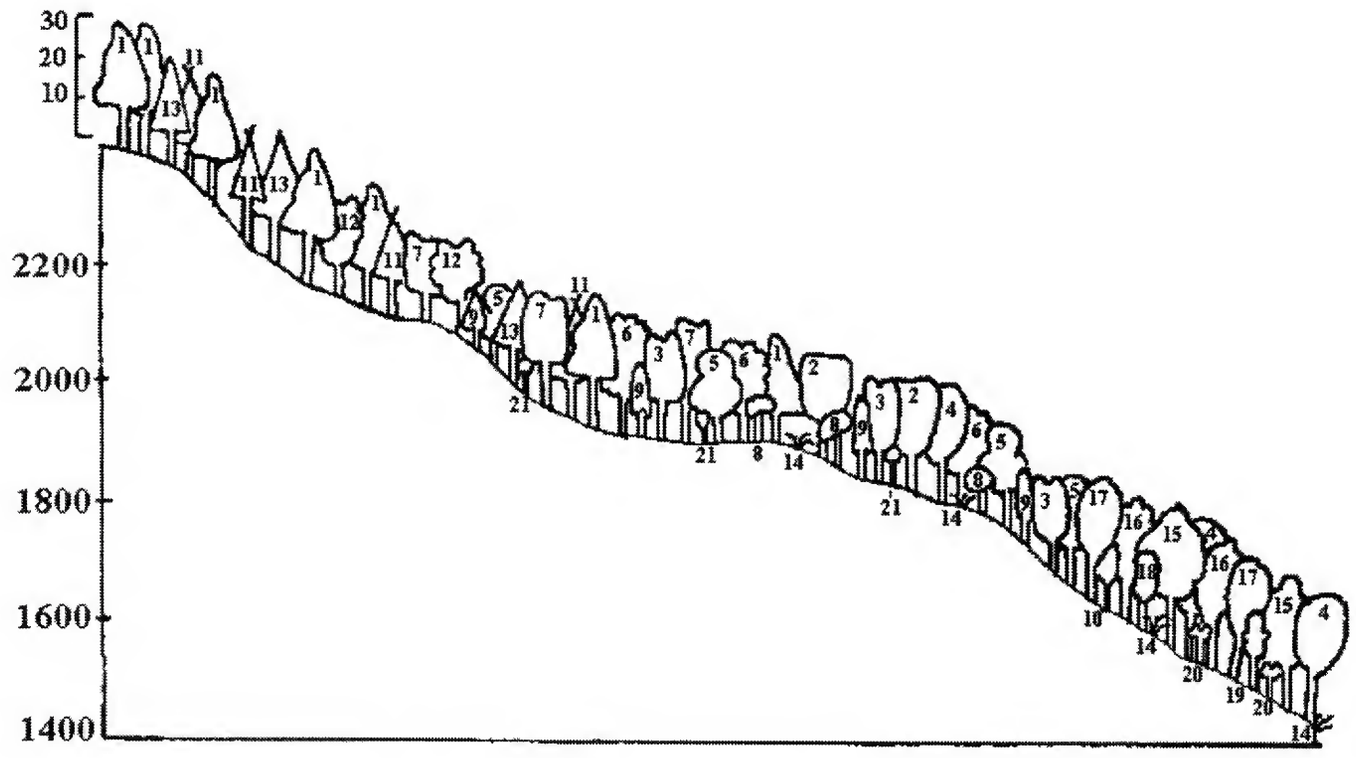


Figure 3.30. Distribution of cloud forest vegetation (bosque mesófilo de montaña) in Mexico. From Luna Vega et al. (2001). Used with permission of Editorial INBio, Santo Domingo de Heredia, Costa Rica.

Veracruz, and its defining features will be discussed more fully in the section on South America, where diminishing stands of the largest extent of the community remain scattered across the Amazon Basin. It is noted here, however, that the essential elements of a rain forest are evident in the Veracruz community. Its extent and diversity increase in the lowlands to the south, while to the north, modified versions reach ~22°N near Tampico and individual elements extend varying distances farther north, notably some palms to southern Florida and *Rhizophora* to east-central Florida at latitude ~29°N (I: pp. 25–26).

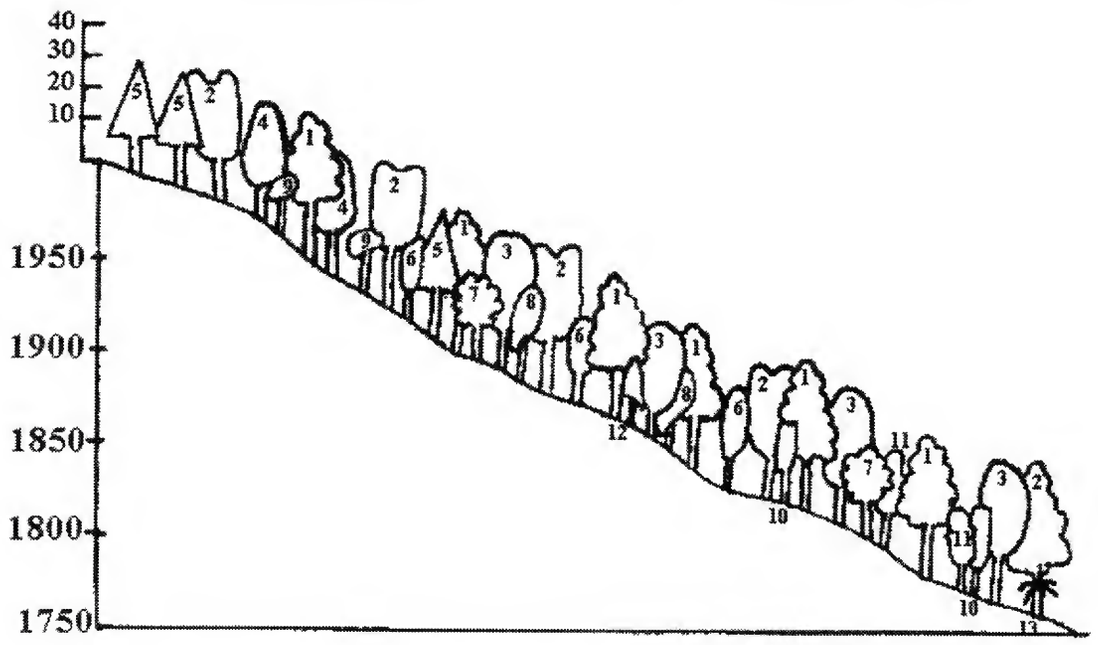
The lowland occurrence of the rain forest often places it immediately inland to coastal basins of deposition and adjacent to mangrove swamps. The poorly consolidated sediments of the forest soils, slow rates of deposition, frequent flooding, and intense microbial activity are not suited for the preservation of megafossils within the rain forest (Prologue Fig. 1). However, lignites and associated fine-grained sediments accumulating in the adjoining mangrove habitats often contain plant microfossils of the adjacent plant formations. Therefore, the history of the lowland Neotropical rain forest is comparatively well known from its northernmost occurrence in Veracruz to the area of its greatest extent in the Amazon Basin, and from sediments ranging in age throughout the Cenozoic (Morley, 2000). However, a factor not widely acknowledged in reconstructing the history of this community is that during warm intervals favoring maximum extent of the rain forest, ice was less, sea levels were higher, and lowland basins and coastal areas were flooded. Thus, in times of maximum climate suitability, the physical habitats available to the lowland rain forest were more restricted. In Veracruz, for example, a sea level higher by ~120 m would bring the coastline close to the slopes occupied by the wet lowland phase of the lower to upper montane broad-leaved forest. The Amazon Basin was partly flooded swamp during much of the Cenozoic. It was when sea levels were moderate, lowlands were being partly drained, and warm moist climates extended over vast expanses of the landscape, as in the Paleogene, that lowland Neotropical rain forest reached its maximum extent.

Lower to upper montane broad-leaved forest (cloud forest; mossy forest; elfin forest; pre-, lower-, and upper-montane rain forest; temperate deciduous forest; Velázquez et al., 2000)—Immediately behind the lowland tropical rain forest, there is a complex of broad-leaved forest types (selvas) that occupy the low (~700 m) to mid (2700 m) elevations of Mexico, and occur in comparable habitats throughout Latin America (Figs. 3.29–3.33). They include associations distinguished by decreasing height and increasing degrees of deciduousness depending primarily on MAP (amounts, extremes, seasonality). Names were given to each of these intergrading associations by Miranda and Hernández X. (1963), and the names are



Eloxochitlán

1. *Cupressus benthamii*
2. *Carpinus caroliniana*
3. *Quercus sartorii*
4. *Tilia houghii*
5. *Magnolia schiedeana*
6. *Quercus germana*
7. *Quercus affinis*
8. *Bahuinia chapulhuacana*
9. *Clethra mexicana*
10. *Styrax glabrescens*
11. *Pinus pseudostrobus*
12. *Quercus crassifolia*
13. *Pinus patula*
14. *Ceratozamia mexicana*
15. *Meliosma alba*
16. *Persea americana*
17. *Quercus acutifolia*
18. *Clethra alcocerii*
19. *Ocotea klotzschiana*
20. *Perrottetia ovata*
21. *Rhamnus pompana*



Tlahuelompa

1. *Fagus grandifolia* ssp. *mexicana*
2. *Quercus sartorii*
3. *Quercus trinitatis*
4. *Quercus eugeniifolia*
5. *Pinus patula*
6. *Clethra mexicana*
7. *Magnolia schiedeana*
8. *Ostrya virginiana*
9. *Befaria laevis*
10. *Cleyera theaeoides*
11. *Ocotea klotzschiana*
12. *Ternstroemia huasteca*
13. *Cyathea fulva*

Figure 3.31. Profiles through cloud forest vegetation in Eloxochitlán and Tlahuelompa, Hidalgo, Mexico. From Luna Vega et al. (2001). Used with permission of Editorial INBio, Santo Domingo de Heredia, Costa Rica.

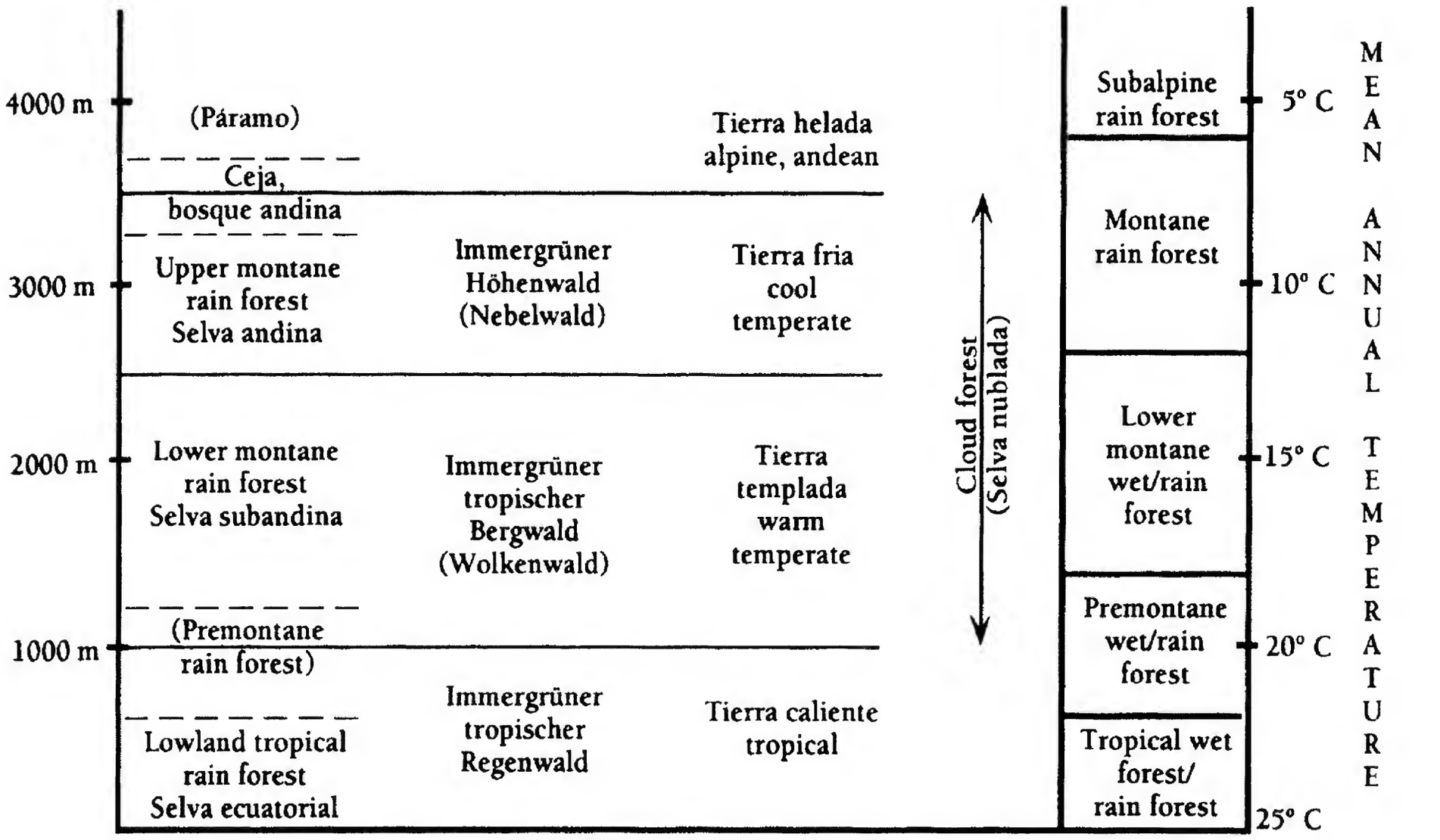


Figure 3.32. Generalized diagram and terminology for Neotropical plant elevational zones. Right-hand columns are the life zones of Holdridge (1967; Holdridge et al., 1971) and the corresponding MATs. From Webster (1995), based on Lauer (1986). Reprinted by permission from the New York Botanical Garden, Bronx, and Barbara Webster.

used in modified form for the extant vegetation of Mexico by Rzedowski (1978), Nueva Galicia by Rzedowski and McVaugh (1966), and Veracruz by Gómez-Pompa (1973). These communities for Veracruz are listed in Table 3.3 and Appendix 1.1. They include the tall semi-evergreen selva, medium semi-evergreen selva, low semi-evergreen selva, and low deciduous selva. The names are applied to mesic forests between the lowland rain forest and the high-altitude páramo. The system of Beard (1944, 1955) is used by Breedlove (1973, 1981, Appendix 1.2; see Figs. 3.54, 3.55) for the vegetation of Chiapas.

As noted earlier, in addition to stature and composition, it is also possible to classify communities by a combination of the elevational zone they occupy (premontane, lower montane, upper montane, subalpine, alpine) and the moisture characteristics of each zone (dry, moist, wet). This system developed by Holdridge (1947a, 1967; Holdridge et al., 1971; Fig. 3.1) has been applied widely, including the vegetation of Mexico. Modifications of the Holdridge model, as they pertain to the mesic communities between the lowland tropical rain forest and the páramo, are those of Grubb (1974), Lauer (1986, 1989), Hartshorn and Peralta (1988), Cleef et al. (1984), and Gradstein and Frahm (1987). The lower montane wet forest, montane moist forest, subalpine moist forest, and other life zones (Fig. 3.1) are included here under the lower to upper montane broad-leaved forest.

At elevations between ~1000 and 3000 m, MAT ranges from 22° C to <10° C, and moisture ascending from the lowlands begins to condense to produce fog; hence, the name cloud forest for one of the associations (Kappelle & Brown, 2001; Luna Vega et al., 2001). The MAP (2000–4000 mm) and high atmospheric humidity allow the growth of numerous epiphytes (lichens, mosses, ferns, bromeliads), and this is the basis for another name, the mossy forest. At the uppermost limit of the forest, the trees may be stunted and gnarled by the cold, drier winds and form an elfin forest association. Frequently these mesic, moist to wet, mid- to upper-altitude associations of the montane broad-leaved forest are referred to collectively as montane rain forest.

There are an estimated 30,000 species of vascular epiphytes in the world (Madison, 1977; see also Webster, 1995, p. 59), in addition to bryophytes, fungi, and algae, and these give a characteristic aspect to the cloud forest. However, the spores, other than those of the ferns, have not been widely studied. The spores of bryophytes have been especially neglected, even though surveys of modern types (Boros & Járai-Komlódi, 1975; Rushing, 1985) indicate many can be recognized to genus (Jarzen, 1979; Materri, 1988). A spore and pollen signature showing the kinds and amounts of prominent epiphytes could aid in recognizing a cloud or mossy forest association.[4]

As a result of the multiple schemes applied to the classification of the lower to upper montane broad-leaved forest formation and the naming of its associations, a formidable nomenclature has developed in which the definition of the components varies according to stature, deciduousness, com-

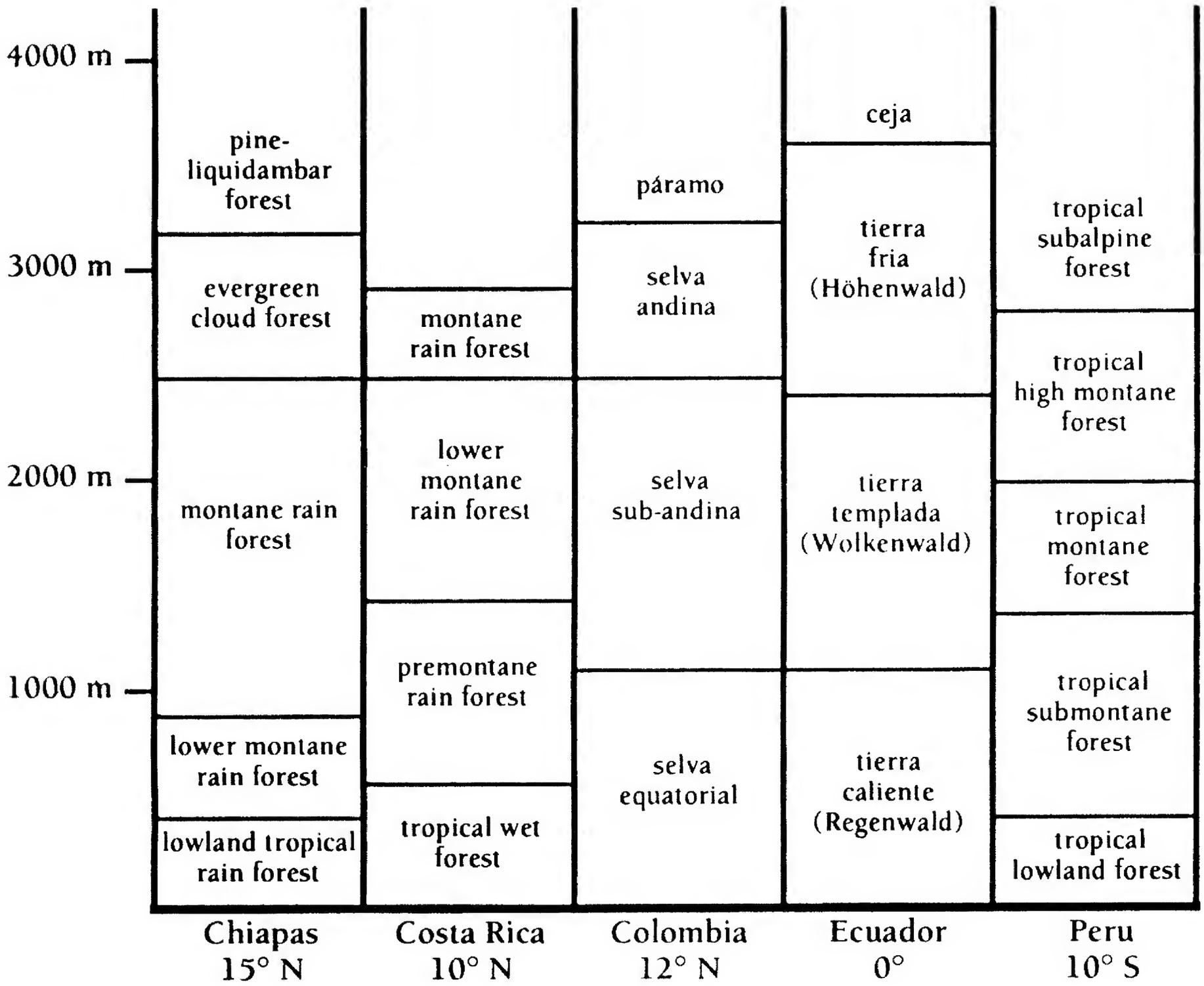


Figure 3.33. Elevational transects through montane rain forest sites (montane broad-leaved forest) in Chiapas (Mexico), Costa Rica, Colombia, Ecuador, and Peru. From Webster (1995). Reprinted by permission from the New York Botanical Garden, Bronx, and Barbara Webster.

position, elevational range, and climate. The ecotones are transitional, and the composition at the lower limits overlaps with the lowland rain forest. This problem is addressed by recognizing a premontane rain forest with an elevational range of ~500–1400 m. The upper limits may be transitional with the páramo, and this gradational community of low scattered trees at ~3200–3500 m is called ceja. In its driest phases, the lower montane broad-leaved forest grades into the tropical dry forest and the low deciduous selvas of Miranda and Hernández X. (1963).

Finally, the composition within the montane rain forest is different at its lower and upper limits. This difference has been recognized by subdividing the formation into a lower montane rain forest (~1400–2500 m) with numerous tropical representatives of the Annonaceae, Melastomataceae, and Arecaceae (Palmae), and an upper-montane rain forest (2500–3500 m) with temperate taxa such as *Podocarpus*, *Alnus*, *Drimys*, *Weinmannia*, Magnoliaceae, and others. Webster (1995) provides a summary of these vegetation types, and his diagrams are shown in Figs. 3.32 and 3.33. An overview of the montane broad-leaved forest, montane rain forest, cloud forest, mossy forest, and elfin forest for the Neotropics is given by Churchill et al. (1995) and Kappelle and Brown (2001), and for broader regions of the world by Hamilton et al. (1995). The generic composition of many associations within the montane broad-leaved forest formation overlaps to the extent that it would be difficult to distinguish most of them in a fossil assemblage, and for present purposes they are grouped together into the lower to upper montane broad-leaved forest.

The term paratropical (meaning "nearly" or "almost") rain forest of Wolfe (1979) has been used to characterize some Late Cretaceous and Paleogene paleocommunities of northern North America (I: pp. 148–150 et seq.). This paleovegetation type is approximately equivalent to the lowest elevation, wettest phases of the modern lower montane broad-leaved forest—the premontane-lower montane rain forest in the Holdridge system, and the tall semi-evergreen to medium semi-evergreen selvas of Miranda and Hernández X. (1963). Among plant

microfossils reported from the Cenozoic of Mexico that may represent this forest are *Lycopodium*, *Selaginella*, *Cyathea*, *Pteris* (tropical moist forest), *Sphaeropteris–Trichipteris*, *Podocarpus*, *Alchornea*, *Allophylus* (secondary), cf. *Astrocaryum*, cf. *Bernardia* (secondary), *Bursera*, *Caesaria*, *Cedrela*, cf. *Chamaedorea*, *Cupania*, *Daphnopsis*, *Faramea*, *Guarea*, *Gustavia*, *Hampea*, *Hibiscus*, cf. *Hiraea*, *Ilex*, *Iresine*, *Matayba*, *Myrcia*, cf. *Paullinia* (Fig. 3.34), *Protium*, *Quercus*, *Rajania*, cf. *Sapium*, *Securidaca* (secondary), *Serjania* (Fig. 3.35), *Spathiphyllum*, *Symphonia*, *Terminalia* type, cf. *Tetrorchidium*, and *Ulmus*.

The cordillera of Mexico were substantially uplifted in the late Cenozoic, and global temperatures lowered during the same interval. This suggests an origin, or considerable expansion, of modern cloud forests in relatively recent times. It is noteworthy that endemism among cloud forest taxa is low at the generic level and high at the species level, consistent with recent and rapid speciation (Webster, 1995). Recognition of such correspondence between geological and biological observations moves studies of tropical biology toward the ecosystem level as defined in this text.

Deciduous forest (bosque mesófilo de montaña; oak-*Liquidambar* forest) association: One exception to the lack of recognizable associations within the lower to upper montane broad-leaved forest formation in fossil assemblages is one characterized by a number of northern temperate deciduous elements (Fig. 3.36). Along the east-facing slope of the Sierra Madre Oriental in Veracruz at an elevational zone between ~1000 and 2700 m, the climate is similar to that at progressively lower elevations toward the Appalachian Mountains to the north. For example, at Greensboro, North Carolina, at an elevation of 273 m, the MAT is 14.6° C, while in the state of Veracruz, Mexico, at elevations of ~1600 m, the MAT is ~15° C. Similar conditions also exist northward into the state of Tamaulipas (Puig & Bracho, 1987); westward along the west-facing slopes of the Sierra Madre Occidental; and southward at more local sites in the Sierra Madre de Chiapas (Breedlove, 1973, 1981; ~3200–3600 m; see Fig. 3.55), in the highlands around Bluefields, Nicaragua, and with progressively fewer species at higher elevations into South America. The comparable mesic conditions that exist in the eastern United States and in the uplands of eastern Mexico are disrupted by the lowland Gulf of Mexico Coastal Plain and the Chihuahuan Desert of south Texas and northern Mexico. However, fluctuating climates have periodically removed or reduced this arid barrier, allowing interchange between the biotas, and many of the same or closely related plants and animals occur disjunctly in the two areas (I: ch. 9; Martin, 1955, 1958; Martin & Harrel, 1957; Miranda & Sharp, 1950; for other references, see Rzedowski, 1978, pp. 315–316). The community in eastern Mexico shows the expected transitions as some elements at the upper limits intermingle with the montane coniferous forest, and others at the lower limits extend into the lowland Neotropical rain forest. One of the last remaining remnants of the Mexican deciduous forest is in Veracruz at Huatusco, near Jalapa. Here the forest includes such tropical families as the Cyatheaceae (a family of tree ferns), Arecaceae (palms), Annonaceae, and Melastomataceae, together with *Lycopodium*, *Pteridium*, *Abies*, *Pinus*, *Acer*, *Alnus*, *Carpinus*, *Cornus*, *Diospyros*, Ericaceae, *Fagus*, *Ilex*, *Juglans*, *Liquidambar*, *Magnolia*, *Myrica*, *Prunus*, *Ostrya*, *Platanus*, *Populus*, *Quercus*, *Rubus*, *Salix*, *Sambucus*, *Smilax*, *Ulmus*, and others. Mixed with these are temperate plants of Latin American origin such as *Podocarpus*, *Alfaroa*, *Drimys*, *Oreomunnea*, and *Weinmannia* as well as more warm-temperate to subtropical genera such as *Cyathea*, *Clethra*, *Eugenia*, *Hedyosmum*, *Heliconia*, *Meliosma*, *Oreopanax*, *Peperomia*, and *Persea*. The few remaining vestiges of the deciduous forest association in Mexico are limited in extent and are rapidly disappearing. It presently constitutes ~0.5% of the vegetation cover of the country.

The deciduous forest association is important in the study of Neotropical vegetation history because it is an identifiable community that occupies a rather specific elevational and climatic zone. Furthermore, it occurs along mountain slopes,

Figure 3.35. Leaves and flowers of *Serjania* sp. From TROPICOS. Used with permission of the Missouri Botanical Garden, St. Louis.

Figure 3.34. Leaves and fruits of *Paullinia* sp., Panama. From TROPICOS. Used with permission of the Missouri Botanical Garden, St. Louis.

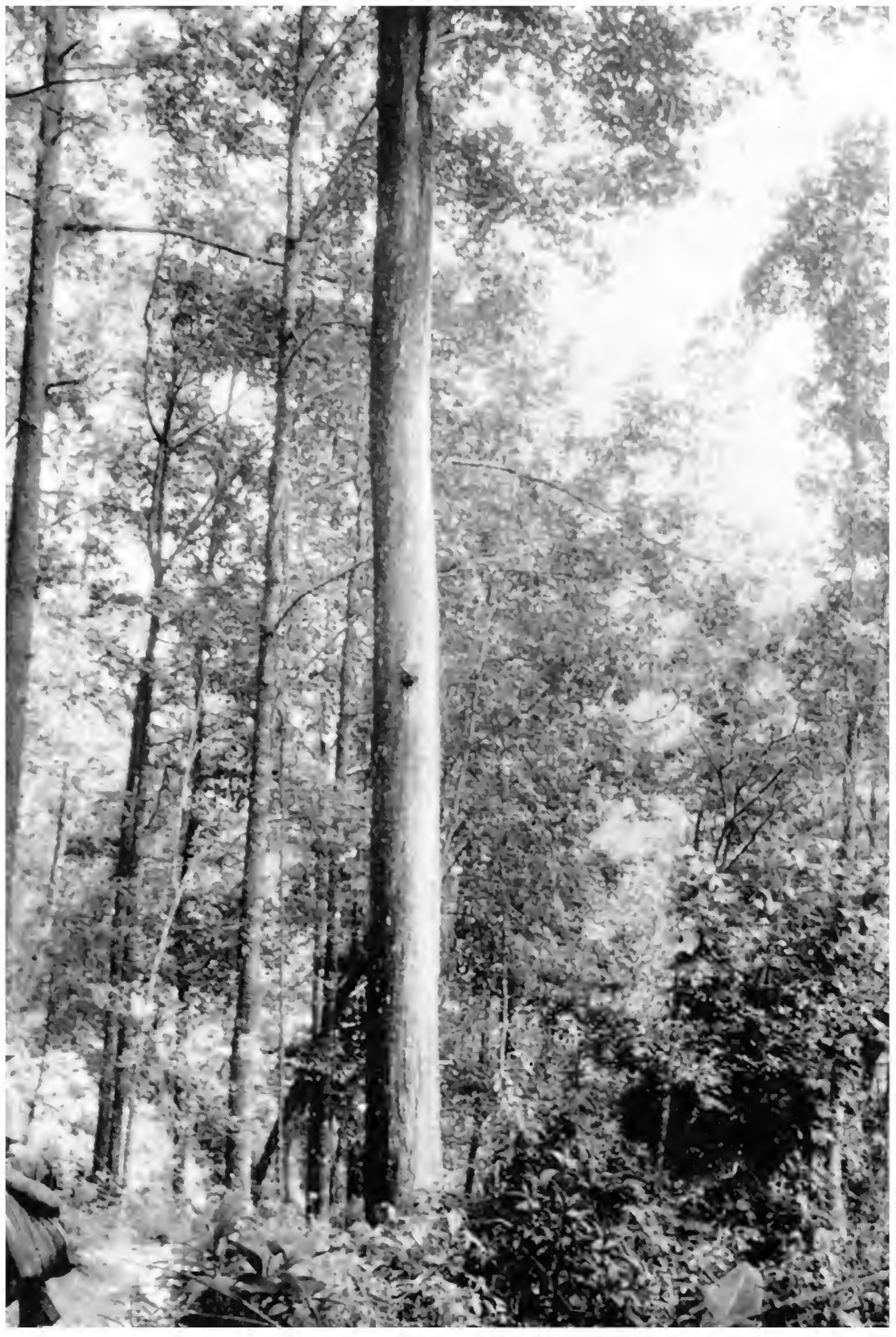


Figure 3.36. Deciduous forest with *Liquidambar macrophylla*, Sierra Madre de Chiapas, Mexico. From Wagner (1964). Photograph by Aaron A. Sharp.

meaning that ecotones are relatively sharp, and that slight changes in MAT or MAP cause exaggerated shifts in its position bringing the association markedly downslope or upslope. These movements are recorded in Tertiary lignites accumulating in lowland depositional basins, and in spore and pollen assemblages from Quaternary bog and lake sediments.

As noted previously, there are few Late Cretaceous (Maastrichtian) or Tertiary megafossil floras in Mexico studied recently, although there are some in the states of Coahuila, Sonora, and Puebla (Chapter 4). Microfossil assemblages are more frequent, and the following genera of the deciduous forest association are reported from the Cenozoic of Mexico: *Lycopodium*, *Pteridium* type, *Alnus*, *Ilex*, *Juglans*, *Liquidambar*, *Populus*, *Quercus*, and *Ulmus*, as well as more warm-temperate to tropical components such as *Cyathea*, *Podocarpus*, *Eugenia* type, and *Meliosma*. The spore and pollen signature is distinctive, and the Cenozoic history of this community is comparatively well known.

Coniferous forest (pine, oak, pine-oak [included under bosque de coniferas y de *Quercus* in Rzedowski, 1978; bosque de encino (oak); bosque de pino (pine); bosque de pino y encino]; montane coniferous forest associations)—Needle-leaved conifers cover ~15% of the landscape in Mexico or 22.6 million hectares. The most widespread is *Pinus* (~12%; Figs. 3.37, 3.38), frequently occurring on acid, well-drained, porous, dry sandy soils on slopes at mid-elevations between 1500 and 3000 m. It grows in the uplands of Baja California, Sierra Madre Occidental (Fig. 1.6), Sierra Madre Oriental, Transvolcanic Belt, Sierra Madre del Sur, and Sierra Madre de Chiapas. Relatively pure stands of pine occur in the mountains to the north and include *Pinus arizonica*, *P. engelmannii*, *P. oocarpa*, *P. patula*, *P. ponderosa*, and *P. teocote*. At the highest elevations, they are associated with *Picea* and *Abies* in the north (2300–3200 m) and with *Abies* in the mountains to the south (3650 m). Among the 111 species of *Pinus* recognized worldwide (Richardson, 1998), 47 are found in Mexico and Central America, and 35 are endemic, giving the region a greater concentration of species than in any other area of comparable size. The MAT in the pine forest is typically 6°–28° C (average 10°–20° C) and MAP ranges from 350–1000 mm (average 600–1000 mm).

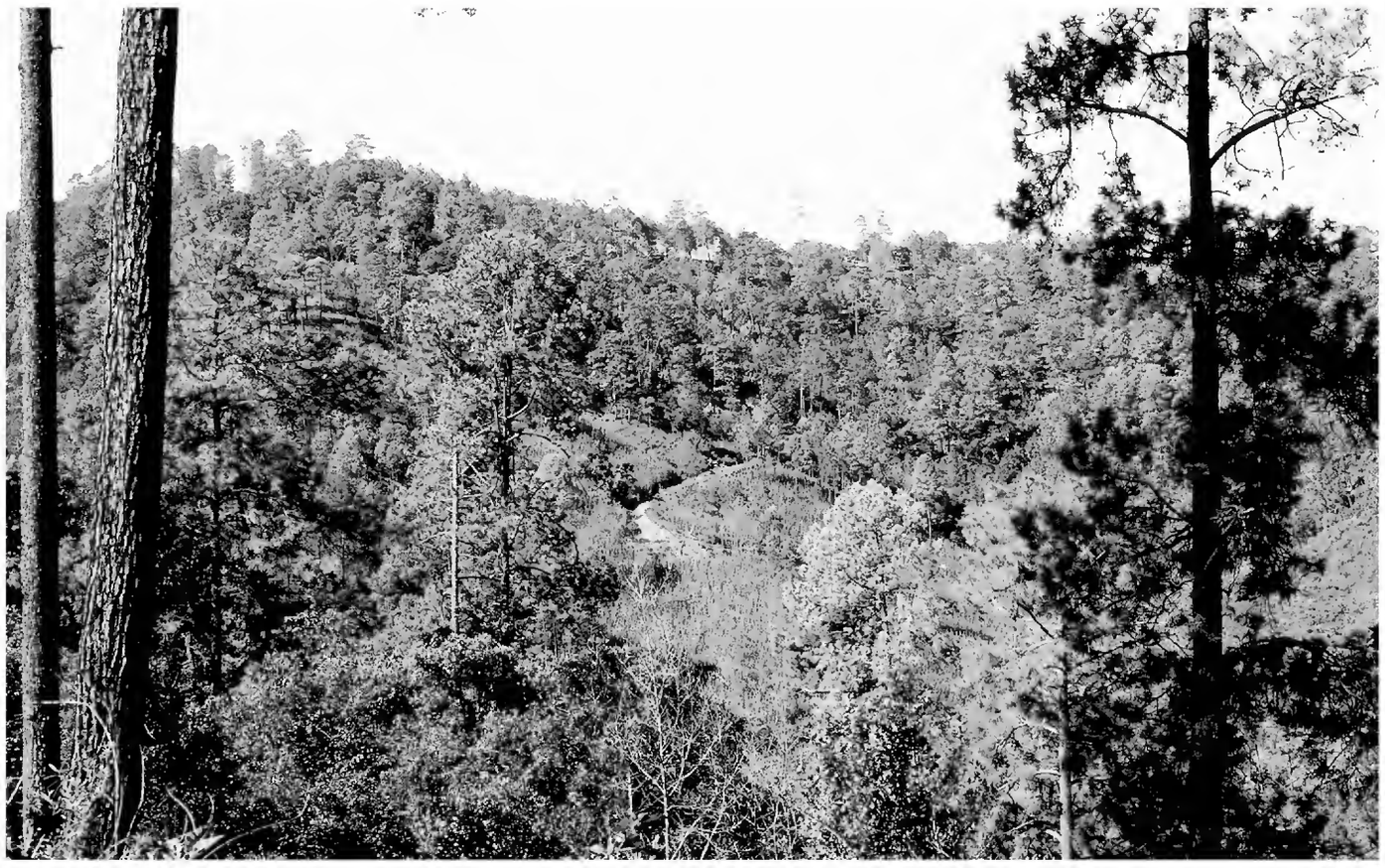


Figure 3.37. Pine forest along Filo de Caballo road, Guerrero, Mexico.

Oaks (encinares) are widespread in Mexico, growing from virtually sea level to 3100 m but most commonly at elevations between 1200 and 2800 m. The 150–200 species of *Quercus* are common on calcareous soils in mid-altitude mesic habitats where occasionally they may be the prominent tree (bosque de encinares, or oak phase within the lower to upper montane broad-leaved forest). More frequently, they are mixed with temperate deciduous elements as part of the deciduous forest (bosque mesófilo de montaña) or with *Pinus* to form the pine-oak forest (bosque de pino y encino). Among the common species are *Quercus acutifolia* (Fig. 3.39), *Q. affinis*, *Q. aristata*, *Q. elliptica*, *Q. laurina*, *Q. mexicana*, *Q. obtusata*, *Q. resinosa*, and *Q. rugosa* associated with *Cupressus*, *Juniperus*, *Pinus*, *Pseudotsuga*, *Alnus*, *Arbutus*, *Buddleja*, *Cercocarpus*, *Crataegus*, *Fraxinus*, *Garrya*, *Juglans*, *Platanus*, *Populus*, and *Salix*. In more moist habitats, they are found with *Clethra*, *Cornus*, *Ilex*, *Oreopanax*, *Styrax*, *Symplocos*, *Xylosma*; the epiphytes *Polypodium*, *Tillandsia*, *Catopsis*, *Peperomia*, and *Laelia*; the orchids *Epidendrum*, *Oncidium*, and *Odontoglossum*; and the hemiparasites *Phorodendron*, *Psittacanthus*, and *Struthanthus*. In the deciduous forest, the common species are *Quercus affinis* and *Q. skinneri*; in the wet, lowland selva alta perennifolia, *Q. oleoides* (Fig. 3.40); in the moister phases of the arid matorral, *Q. laeta*; and in the high-altitude bosque de oyamel (*Abies*, fir) forests, *Q. candicans*. Collectively, the bosques de encinares make up ~5.5% of the vegetation cover of Mexico.

The MAT for the bosque de encinares ranges from ~10°–26° C, but most commonly it is from 12°–20° C with temperatures in the coldest months reaching 0° C. The MAP is from a low of ~350 mm in Sonora to 2000 mm along the coastal plain of the Gulf of Mexico, with a range typically between 600 and 1200 mm.

Quercus is frequently associated with *Pinus* in a complex mosaic that constitutes the principal plant community of mid-elevation temperate habitats in Mexico. The pine-oak forests

Figure 3.38. Vestige of pine forest, state of México, Mexico.

cover ~13.7% of the landscape in Mexico, and collectively oaks, pines, and other conifers occur in various combinations to make up nearly one-third of the vegetation cover of Mexico and adjacent northern Central America. However, except in the most rugged of terranes, the conifer and oak woods now are only highly modified vestiges of their former extent, composition, and grandeur (Fig. 3.38). Examples of the bosque de pino, bosque de encino, and bosque de pino y encino are preserved in the Parque Ecológico Estatal Omiltemi at Chilpancingo in the state of Guerrero (Luna Vega & Llorente Bousquets, 1993).

There is no extensive megafossil record of *Pinus*, *Quercus*, or their associates in Mexico, and the history of the community must be reconstructed primarily from plant microfossils. The pines, oaks, and many other members of this vegetation are anemophilous (wind pollinated), and in contrast to many components of the desert, shrubland/chaparral–woodland–savanna, and grassland formations, they produce large amounts of pollen that are readily preserved and can be distinguished at the generic level. Attempts have been made to identify species

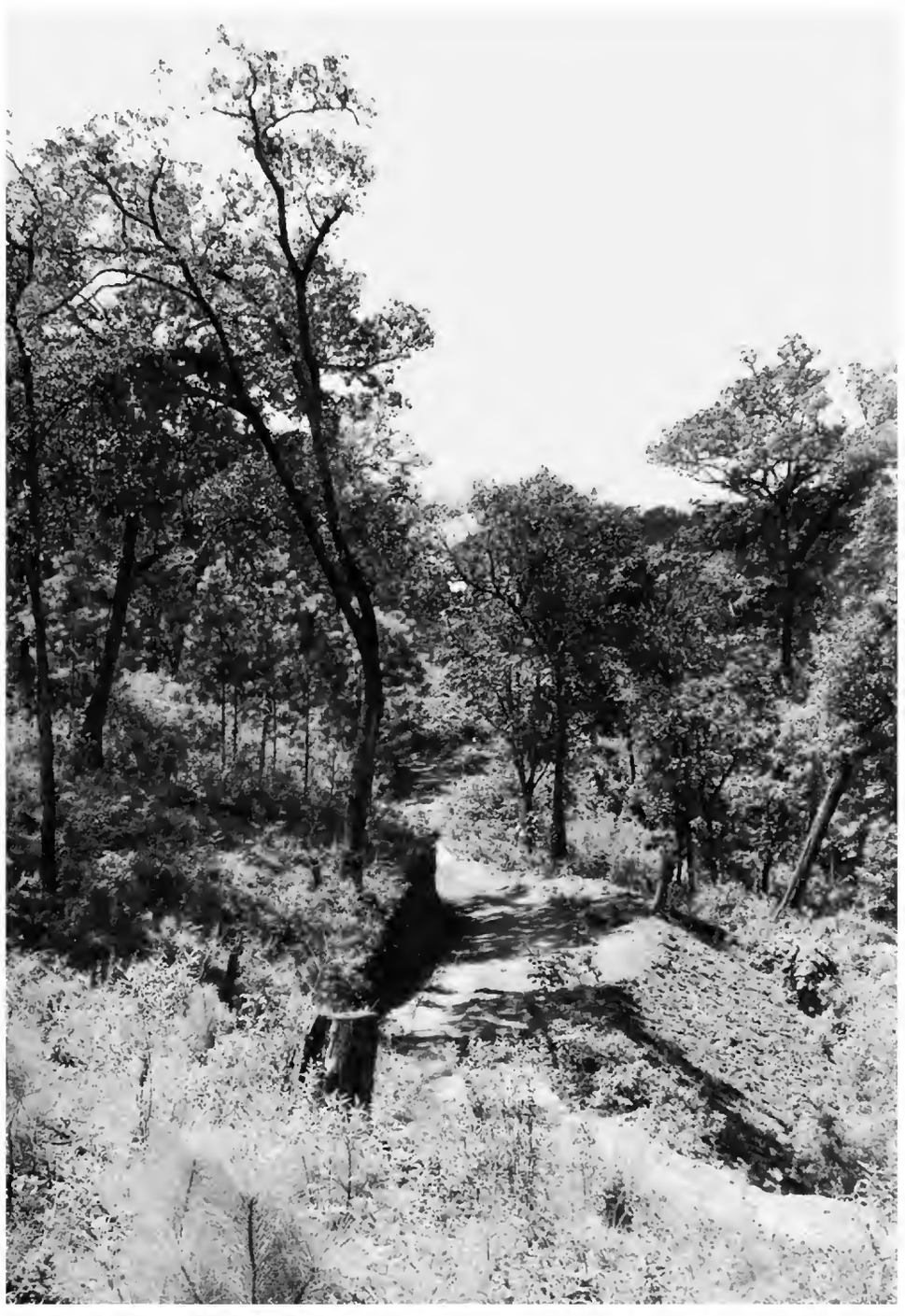


Figure 3.39. Oak woods of *Quercus acutifolia*, *Q. castanea*, and others. Seedlings of pine are present (bottom left) indicating the gradational nature of the pine, oak, and pine-oak forests in many parts of Mexico. Jalisco, Mexico. From Rzedowski and McVaugh (1966). Used with permission of the University of Michigan Herbarium.

Figure 3.40. Leaves and fruits of *Quercus oleoides*, the only tropical lowland species of oak in the Americas. July, Santa Rosa National Park, Guanacaste Province, Costa Rica. From Boucher (1983). Used by permission of the University of Chicago Press, Chicago.

of *Pinus* on the basis of pollen (Cain & Cain, 1944; Ting, 1966), but these have not proved successful. Similarly, fossil pollen of *Quercus* cannot be identified to species. Even so, the Cenozoic history of the pine-oak forest can be reconstructed in relative detail. Members known from the Cenozoic of Mexico are *Pinus*, *Quercus*, *Polypodium* type, *Alnus*, *Juglans*, *Populus*, and *Struthanthus*. In addition, associates frequently grow where the pollen can be carried into nearby basins of deposition by wind or water, and among these are *Arbutus* type (Ericaceae, pollen identifiable to family only), *Ilex*, and *Symplocos*.

The montane coniferous forest association is found in the high elevations of the Sierra Madre Occidental, in the Transvolcanic Belt just below the alpine tundra (páramo), and at a few other more restricted mountain sites. The community extends from the north southward at progressively higher elevations. *Picea mexicana* (Coahuila, Nuevo León, Ledig et al., 2004; = *P. engelmannii* var. *mexicana* fide Taylor et al., 1994) grows in the Sierra Madre Occidental to ~3500 m; *Picea chihuahuana* (Chihuahua, Durango; 2300–3200 m) is found in a few isolated populations (39 stands in three clusters of five to ~100 individuals) in the western mountains (Gordon, 1968) to just south of the Tropic of Cancer (23.5°N); and *P. martinezii* grows in six stands at 2250–2650 m in the Sierra Madre Oriental (Ledig et al., 2000). Along the road from Durango to Mazatlán, near the village of El Salto (state of Durango), *Picea chihuahuana* occurs with *Abies durangensis*, *Cupressus lindleyi*, *Pinus ayacahuite*, *P. durangensis*, *Pseudotsuga menziesii* (Douglas fir), *Prunus serotina*

Figure 3.41. High-altitude pine forest of *Pinus montezumae*, Volcán Tláloc, elevation 3300 m, Puebla, Mexico. From Velázquez et al. (2000). Reprinted with the permission of Cambridge University Press, Cambridge, U.K.

Figure 3.42. High-altitude pine forest of *Pinus rudis* with understory of *Muhlenbergia* sp., Volcán Popocatépetl, Puebla, Mexico.

Figure 3.43. Montane coniferous forest of *Abies religiosa* (oyamel), elevation 3200 m, east of Mexico City. From Wagner (1964). Photograph by Faustino Miranda.

(black cherry), *Quercus castanea*, and *Q. rugosa*. Although the distribution of *Picea* in Mexico today is restricted to a few sites in the northern mountains, during the cool phases of the late Cenozoic it frequently extended as far south as the Transvolcanic Belt of Mexico and into northern Guatemala. *Pseudotsuga menziesii* grows in the Sierra Madre Occidental from the states of Sonora and Chihuahua to Zacatecas; in the Sierra Madre Oriental of Coahuila and Nuevo León; and in the Transvolcanic Belt in Pachuca, Hidalgo, and Puebla. *Pinus montezumae* (Fig. 3.41) and *P. rudis* (Fig. 3.42) are mixed with *Abies religiosa* (bosque de oyamel, 2400–3600 m; Fig. 3.43) in the high-altitude coniferous forests (*P. montezumae* and *P. rudis* are also treated as varieties of *Pinus hartwegii*; see Richardson, 1998). Other gymnosperms grow in drier habitats at lower elevations. *Juniperus* occurs in Baja California and from Tamaulipas to Chiapas in dry open sites between the pine-oak forest and the desert, shrubland/chaparral–woodland–savanna, grassland formations. *Cupressus guadalupensis* is found on the islands of the Gulf of California (Guadalupe), and *C. lindleyi*, a species with very different ecological requirements, grows with *Abies* and *Pinus* in the uplands of southern and central Mexico (e.g., Chiapas, 1800–3000 m). As noted earlier, the zone between the upper limit of mostly coniferous forest and the treeless alpine tundra is marked by scattered trees of short stature to form the transition vegetation types called elfin forest and ceja.

Megafossils representing modern genera of gymnosperms are rare in the Late Cretaceous and Cenozoic of Mexico, but fossil pollen of this anemophilous group is relatively abundant. The pollen of both dominants and some associated genera are frequently blown or washed into lowland basins of depositions (*Abies*, *Picea*, *Pinus*, *Quercus*). These microfossils are important for recording the geologic range of the lineages, and for reconstructing paleoclimates, paleoelevations, and the timing and pathways of migration of temperate elements from the north. They occur in the Tertiary, and their Quaternary record from lakes, bogs, and basin sediments is extensive.

Alpine tundra (páramo; included under pastizal in Rzedowski, 1978; included under páramo in Balslev & Luteyn, 1992)—Above timberline in Mexico, mostly at the contact with the upper montane coniferous forest, there is a treeless, grassy vegetation of alpine tundra, páramo, or zacotonal (Beaman, 1962, 1965; Anaya et al., 1980; Almeida et al., 1994; Popocatépl, Ixtaccíhuatl volcanoes). Common plants include *Muhlenbergia*, *Calamagrostis*, *Festuca*, *Stipa*, and *Trisetum* (Poaceae); *Luzula* (Juncaceae); *Arenaria* and *Cerastium* (Caryophyllaceae); *Cirsium*, *Gnaphalium*, *Oxylobus*, and *Senecio* (Asteraceae, Compositae); *Draba* (Brassicaceae, Cruciferae); *Phacelia* (Hydrophyllaceae); *Lupinus* (Fabaceae, Leguminosae); *Plantago* (Plantaginaceae); *Ranunculus* (Ranunculaceae); *Potentilla* (Rosaceae); and *Eryngium* (Apiaceae, Umbelliferae). All of these belong either to stenopalynous groups or to families so large that the pollen cannot be identified to genus unless the choices can reasonably be limited to ones present in the local modern vegetation (e.g., in some late Quaternary and Holocene sediments). In addition to the cold temperatures, the alpine tundra or páramo is characterized by frequent mist and low-growing vegetation, and it is the farthest removed from the lowland basins of depositions preserving Late Cretaceous and Tertiary plant fossils. For these reasons, the history of the páramo during these intervals is poorly known, but the Neogene and Quaternary record is well preserved in bogs and lacustrine sediments of many highland lakes. Modern páramo is most extensively developed, and its history is best known in the Andes Mountains. It will be discussed further in the vegetation of Colombia.

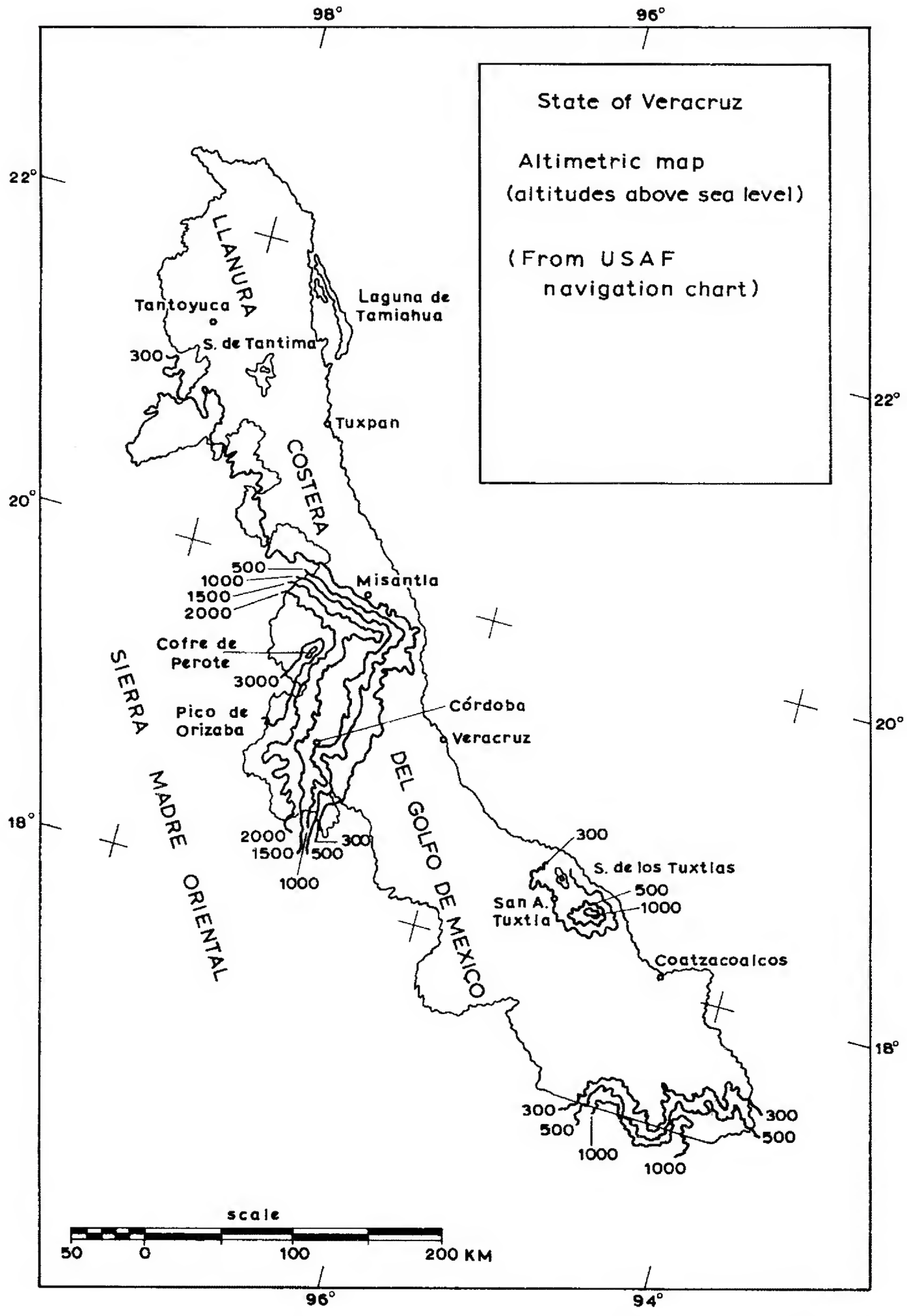


Figure 3.44. Altitudinal map of Veracruz, Mexico. From Gómez-Pompa (1973). Used with permission of Alan Graham.

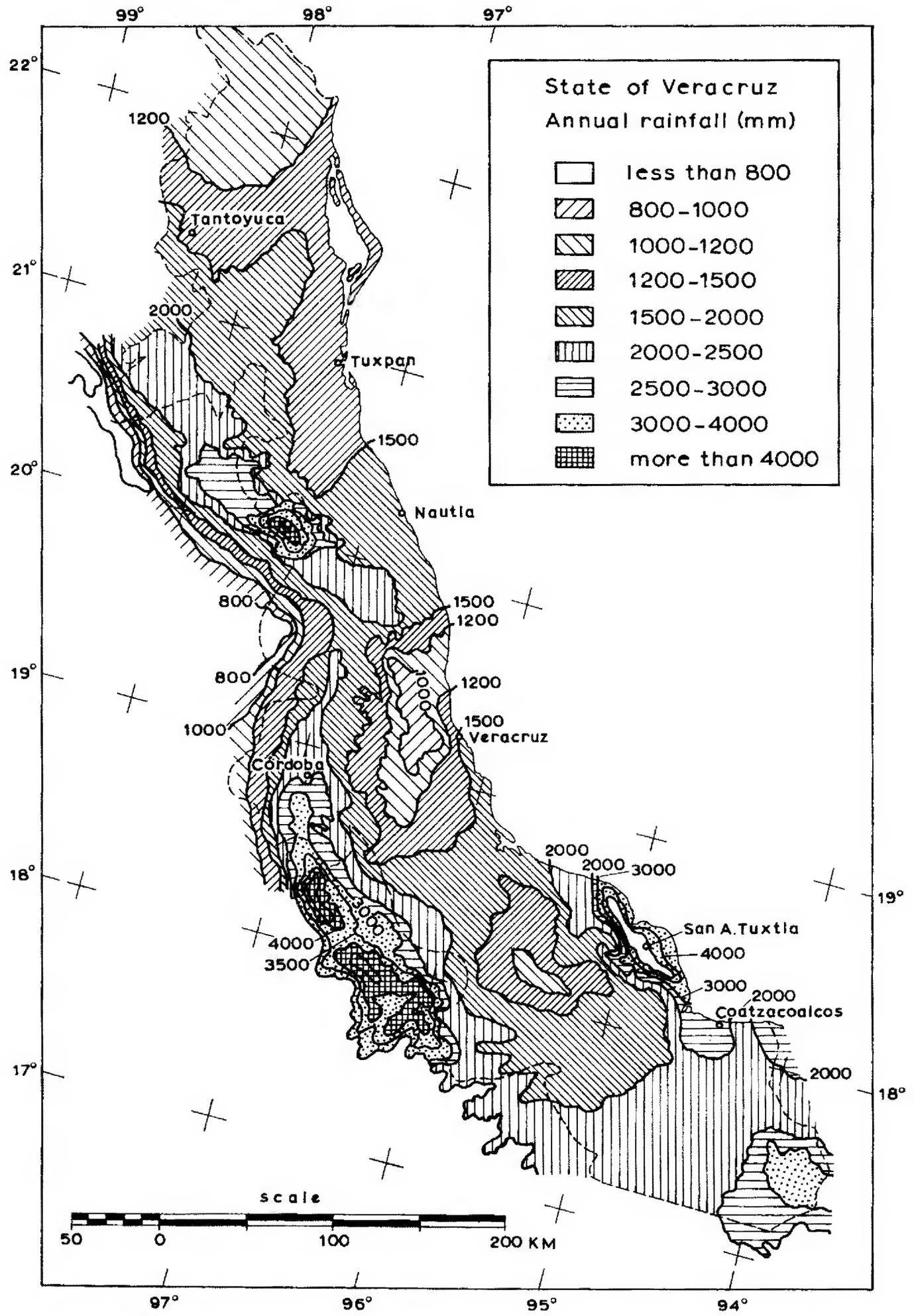


Figure 3.45. Rainfall map of Veracruz, Mexico. From Gómez-Pompa (1973). Used with permission of Alan Graham.

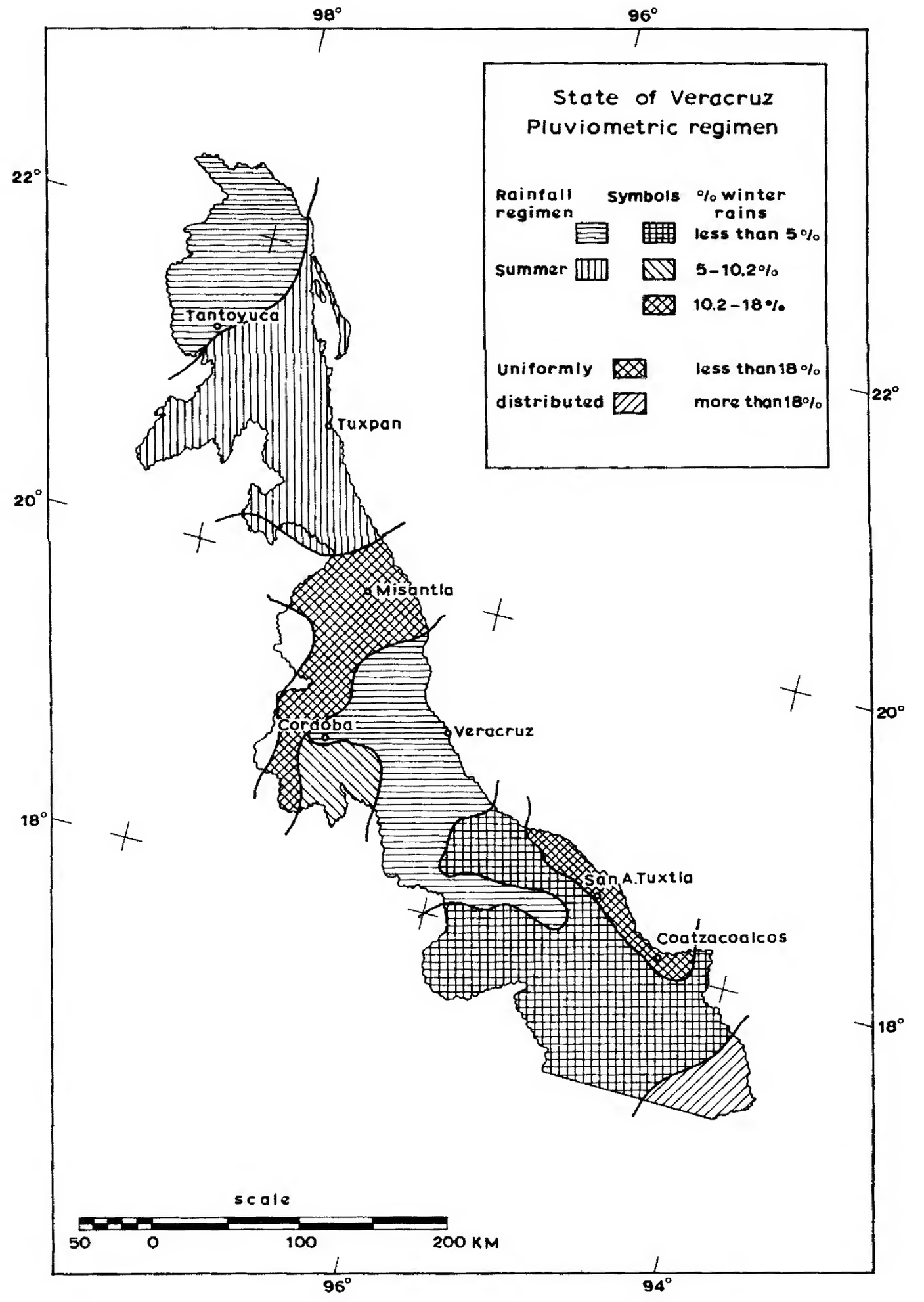


Figure 3.46. Seasonal distribution of rainfall in Veracruz, Mexico. From Gómez-Pompa (1973). Used with permission of Alan Graham.

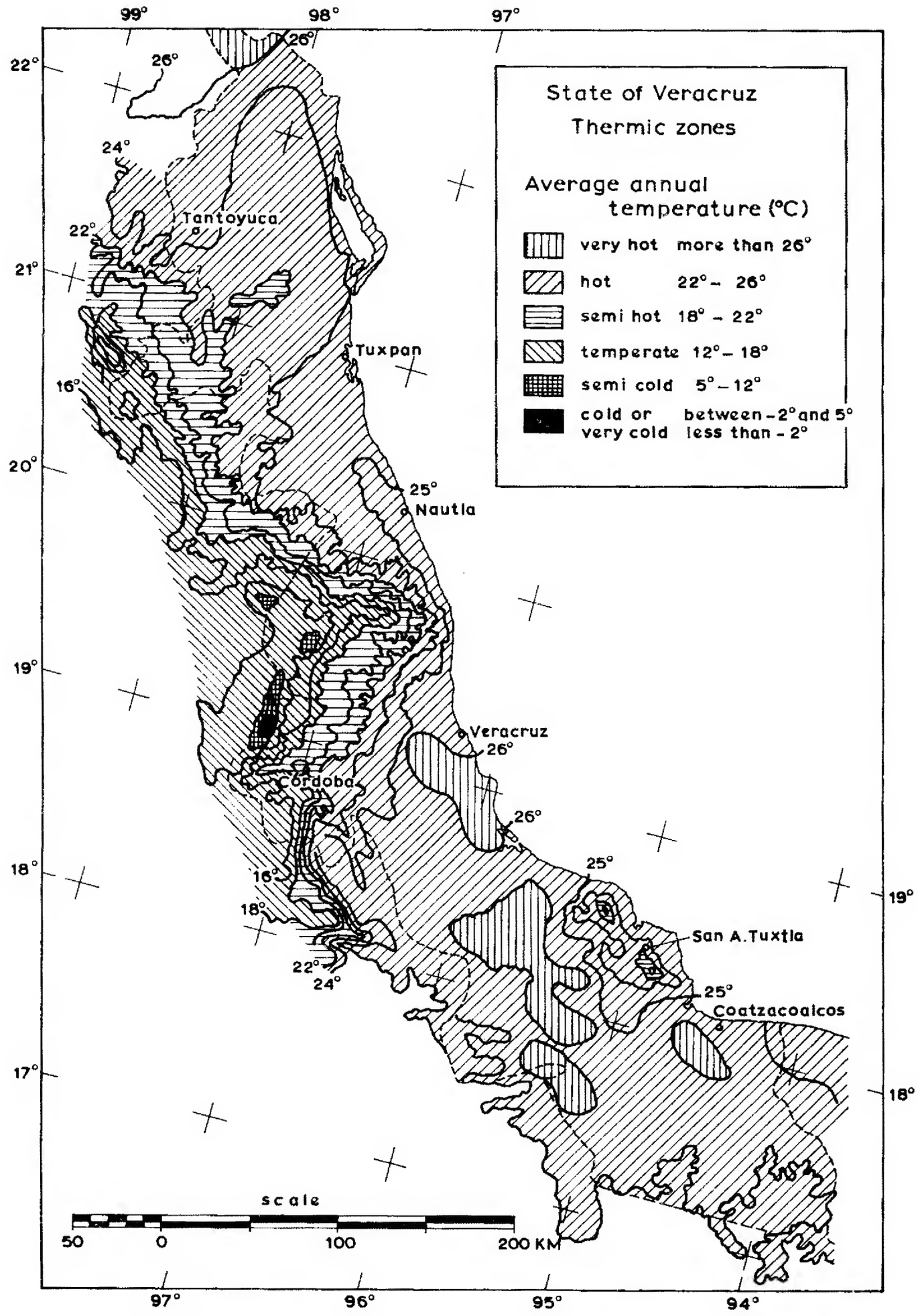
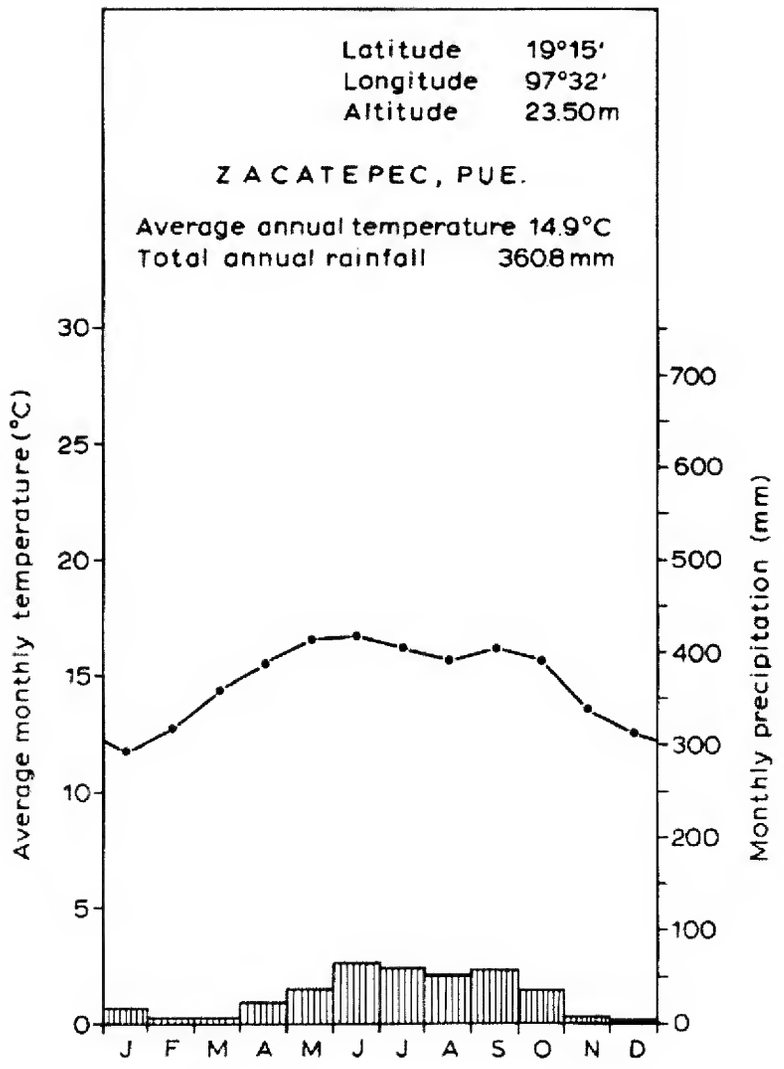
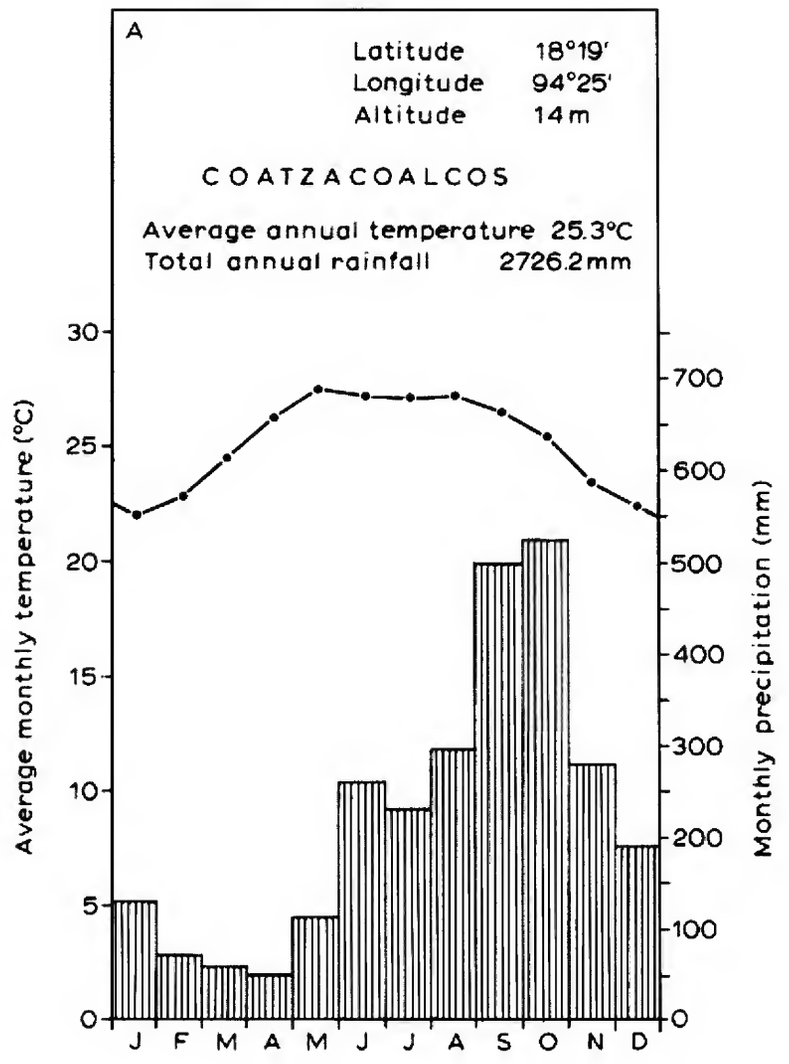
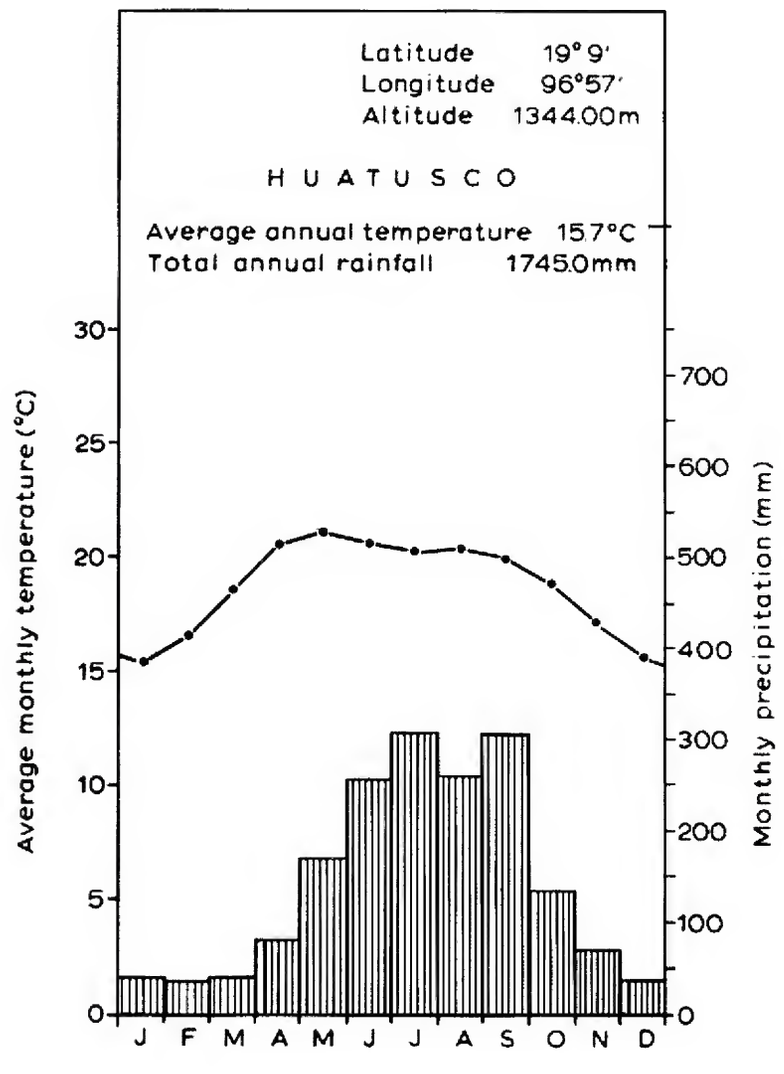


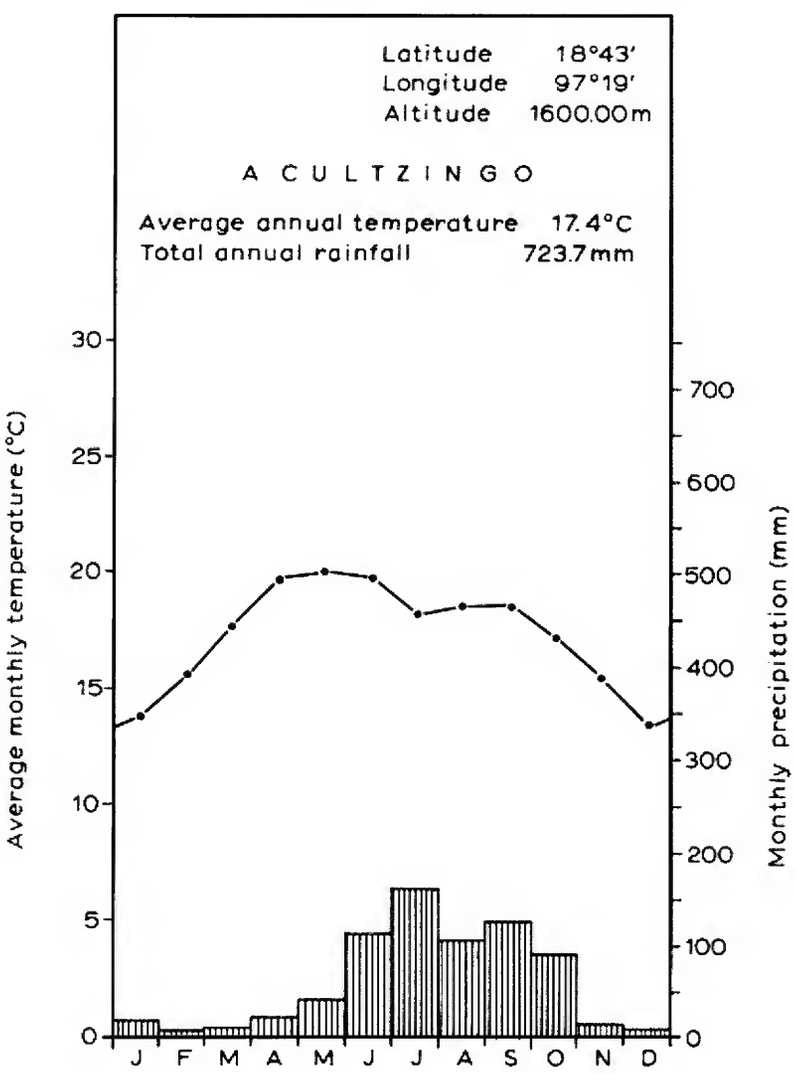
Figure 3.47. Temperature map of Veracruz, Mexico. From Gómez-Pompa (1973). Used with permission of Alan Graham.





Figures 3.48–3.51. Climatic diagrams (climatograms, climatographs) for four sites in Veracruz, Mexico. 3.48 (top left)—Zacatepec, 3.49 (top right)—Coatzacoalcos, 3.50 (bottom left)—Huatusco, 3.51 (bottom right)—Acultzingo. From Gómez-Pompa (1973). Used with permission of Alan Graham.





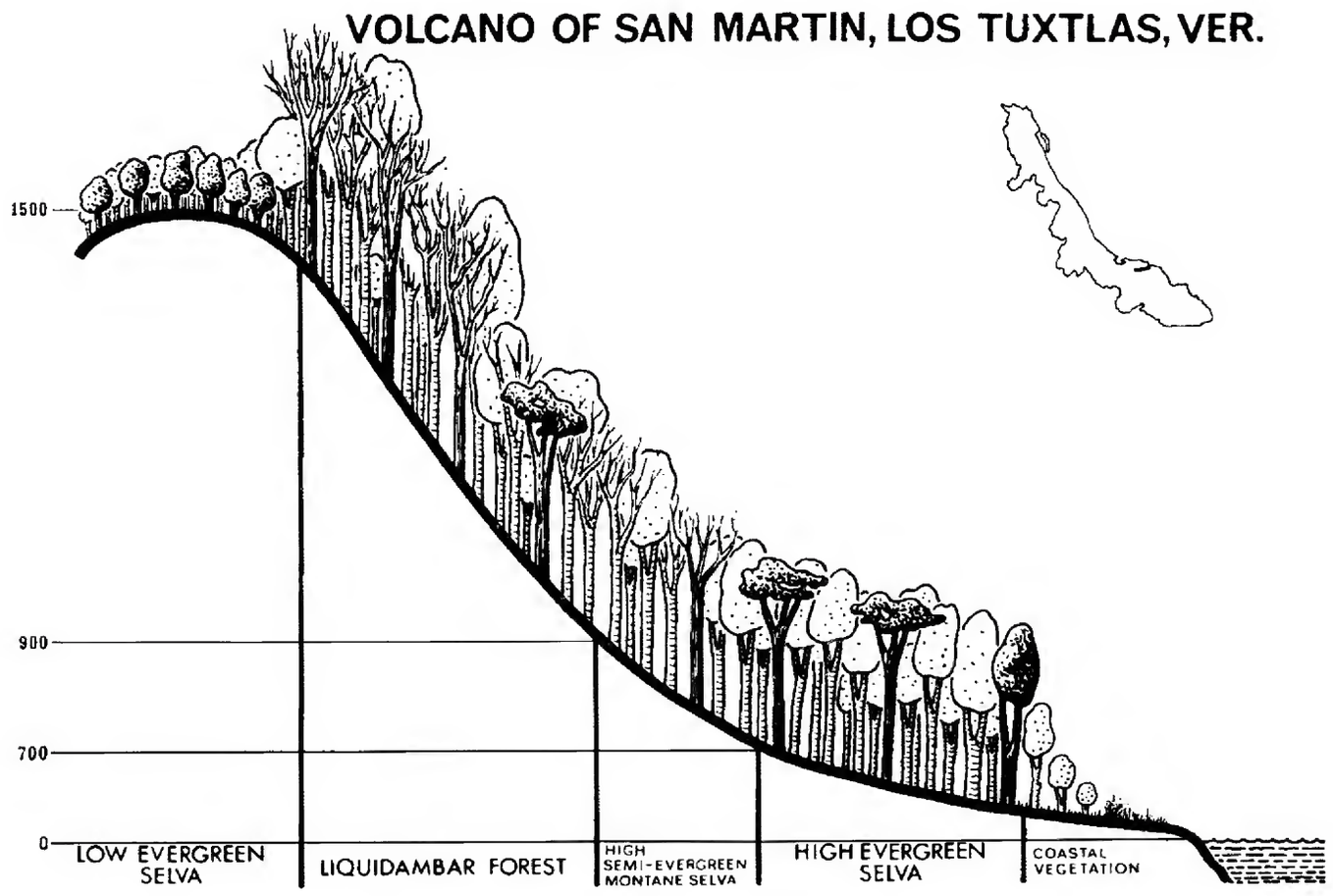


Figure 3.52. Vegetation transect from sea level to the top of Volcán San Martín, Veracruz, Mexico, showing the altitudinal arrangement of the plant communities at that site. From Gómez-Pompa (1973). Used with permission of Alan Graham.

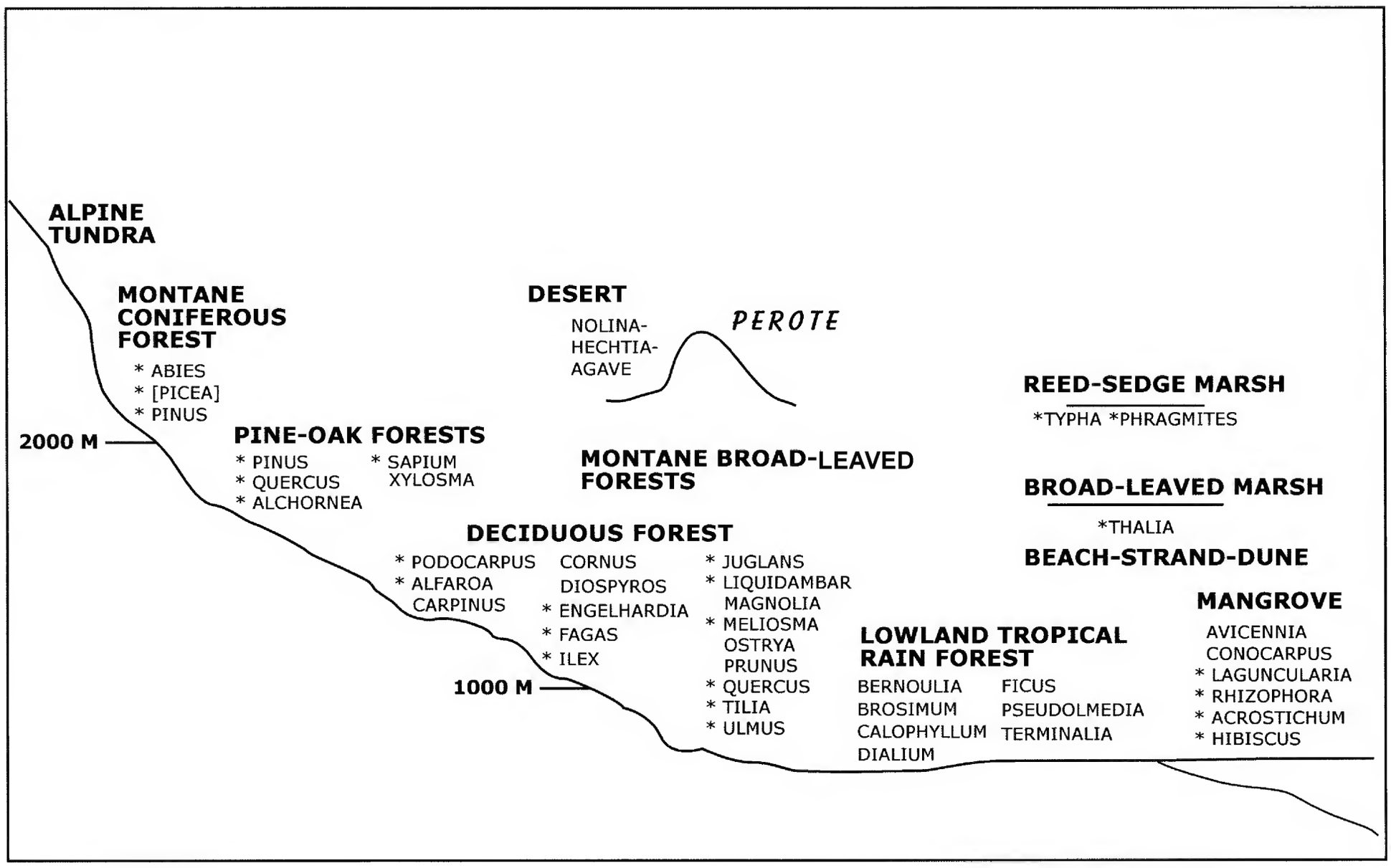


Figure 3.53. Generalized transect from sea level to the highest peak in Veracruz, Mexico, with representative taxa characteristic of each plant formation. Reed–sedge–marsh, broad-leaved marsh, and beach–strand–dune formations are mostly coastal communities behind the mangrove-intertidal zone. Asterisk (*) indicates that the taxon is known from the middle Pliocene Paraje Solo Formation of Veracruz.

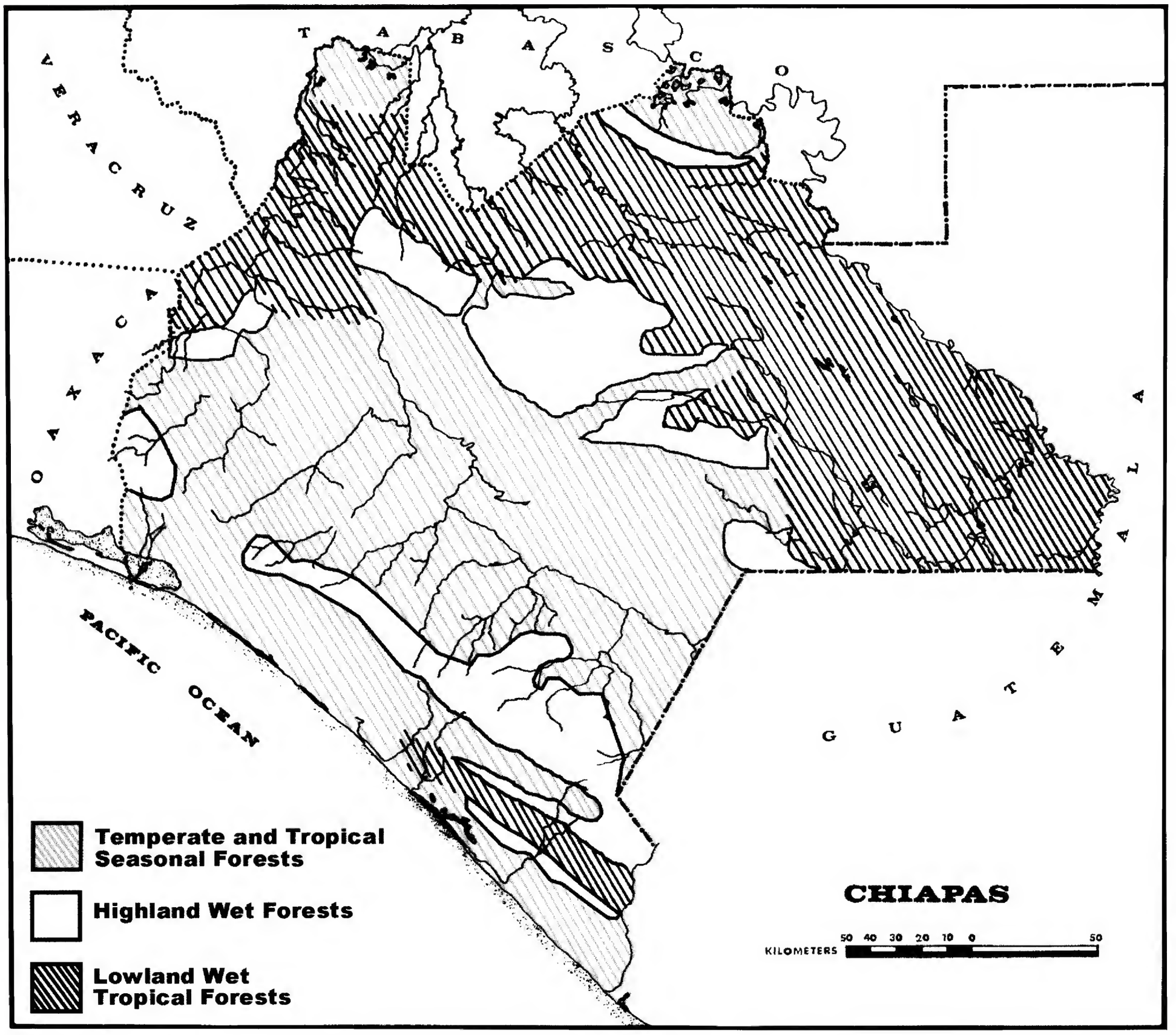


Figure 3.54. Vegetation map of Chiapas, Mexico. Compiled from Breedlove (1981).

Veracruz

Veracruz is an important region of Mexico for the study of tropical vegetation history. The state extends through more than 5° of longitude, from 17°10'N to 22°20'N, and the elevational range is from sea level to the highest point in Mexico at the Pico de Orizaba (5650 m) on the border with Puebla (Fig. 3.44). The considerable longitudinal extent and topographic diversity encompasses a broad array of climates (Figs. 3.45–3.51) and extensive edaphic variation. The result is that Veracruz is physically one of the most diverse and biologically one of the richest states in Mexico. The MAP at UNAM's tropical biological station near Catemaco is 2726 mm. At the other extreme, moisture off the Atlantic Ocean is blocked by the Sierra Madre Oriental west of Perote on the border with the state of Puebla. The MAP on these limestone hills is only 360.8 mm, and the vegetation is a *Nolina–Hechtia–Agave* desert.

Plant fossils are being studied from the Oligocene Pie de Vaca Formation in Puebla, and there is an extensive plant microfossil flora known in the Pliocene Paraje Solo Formation of Veracruz (Chapter 4).

Gómez-Pompa (1973) recognizes 22 vegetation types for Veracruz, and these are summarized in Table 3.3 and Appendix 1.1. Several of the selvas are gradational in response to precipitation, and their differences are mostly too subtle to be detected in the fossil record. An arrangement of the vegetation germane to its geologic history is shown in a transect from the coast to the top of Volcán San Martín (Fig. 3.52), and in an idealized transect depicting the arrangement of the principal communities, their defining members, and fossil representatives in the Paraje Solo flora of southeastern Veracruz (Fig. 3.53).

Table 3.3. Vegetation types of Veracruz, Mexico (after Gómez-Pompa, 1973).

Features	Vegetation type
Vegetation dominated by trees (woody plants >4 m tall)	
Dense multi-dominant tree community, lianas common	
Dominant trees without spines	
Evergreen	
Dominant trees ≥30 m tall	tall evergreen selva (lowland tropical rain forest)
Dominant trees <30 m tall (mostly <10 m)	low evergreen selva
Deciduous	
Trees ≥15 m tall	
Trees >25 m tall	tall semi-evergreen selva
Trees 15–25 m tall	medium semi-evergreen selva
Trees <15 m tall	
<50% deciduous	low semi-evergreen selva
>75% deciduous	low deciduous selva (tropical deciduous forest)
Many dominant trees with spines	low thorn selva (±chaparral)
More open tree community dominated by fewer (usually one or two) tree species, lianas few	
Trees branched	
>50% deciduous	deciduous forest
>75% evergreen	
Land (non-swamp) tree communities	
Broad-leaved	broad-leaved (oak) forest
Needle- or scaled-leaved	
Needle-leaved	needle-leaved forest
Scaled-leaved	scaled-leaved forest
Swamp tree communities	mangrove forest
Trees unbranched	palm stands
Vegetation dominated by shrubs or herbs	
Land (non-aquatic, -marsh, -swamp) shrub or herb communities	
Coastal with marine influence	coastal dune vegetation
Non-coastal	
Dominated by grasses	
Lowland warm areas	savanna
Upland cool and highland cold area	
Soils saline	saline grassland
Soils non-saline	
Temperate areas below 4000 m	temperate grassland
Cold areas above 4000 m	páramo (alpine tundra, puna)
Not dominated by grasses	
Abundance of rosette-leaved plants	*Nolina–Hechtia–Agave* desert
Abundance of thorn shrubs	thorn scrub (chaparral)
Communities partially or totally in water part or all of the year	swamp or aquatic vegetation

Chiapas

Topographic diversity ranges from sea level along the Pacific coast to ~4000 m near the Guatemalan border, and this also provides a diversity of habitats that supports a rich biota. Breedlove (1973, 1981) recognizes 18 plant formations for Chiapas, in addition to second growth and successional forest and shrub associations resulting from disturbance. The system is based on Beard (1944) and is not the same used for adjacent Veracruz (Gómez-Pompa, 1973), Mexico in general (Rzedowski, 1978), or the numerous classifications of other authors (Miranda, 1952–1953; Miranda & Hernández X., 1963; Wagner, 1964; Gómez-Pompa, 1965; Holdridge, 1967; Pennington & Sarukhán K., 1998; Flores M. et al., 1971; Holdridge et al., 1971). A vegetation map of Chiapas is given in Fig. 3.54 compiled from Breedlove (1981), the arrangement of these formations by altitude and precipitation (length of the dry season) is shown in Fig. 3.55, and the plants characteristic of each formation are given in Appendix 1.2.

Spore and pollen studies and catalogs for various modern taxa, communities, or regions of Mexico published since the bibliographies noted in the Prologue include those for Guerrero (Ludlow-Wichers et al., 1991 et seq.); Los Tuxtlas, Veracruz (Lozano-Garcia & Martínez-Hernández, 1990); Tacana, Chiapas (Martínez-Hernández et al., 1993); and Quintana Roo (Palacios-Chávez et al., 1991). Examples of pollen from plants of Mexico and other regions are shown in Figs. 3.56 and 3.57.

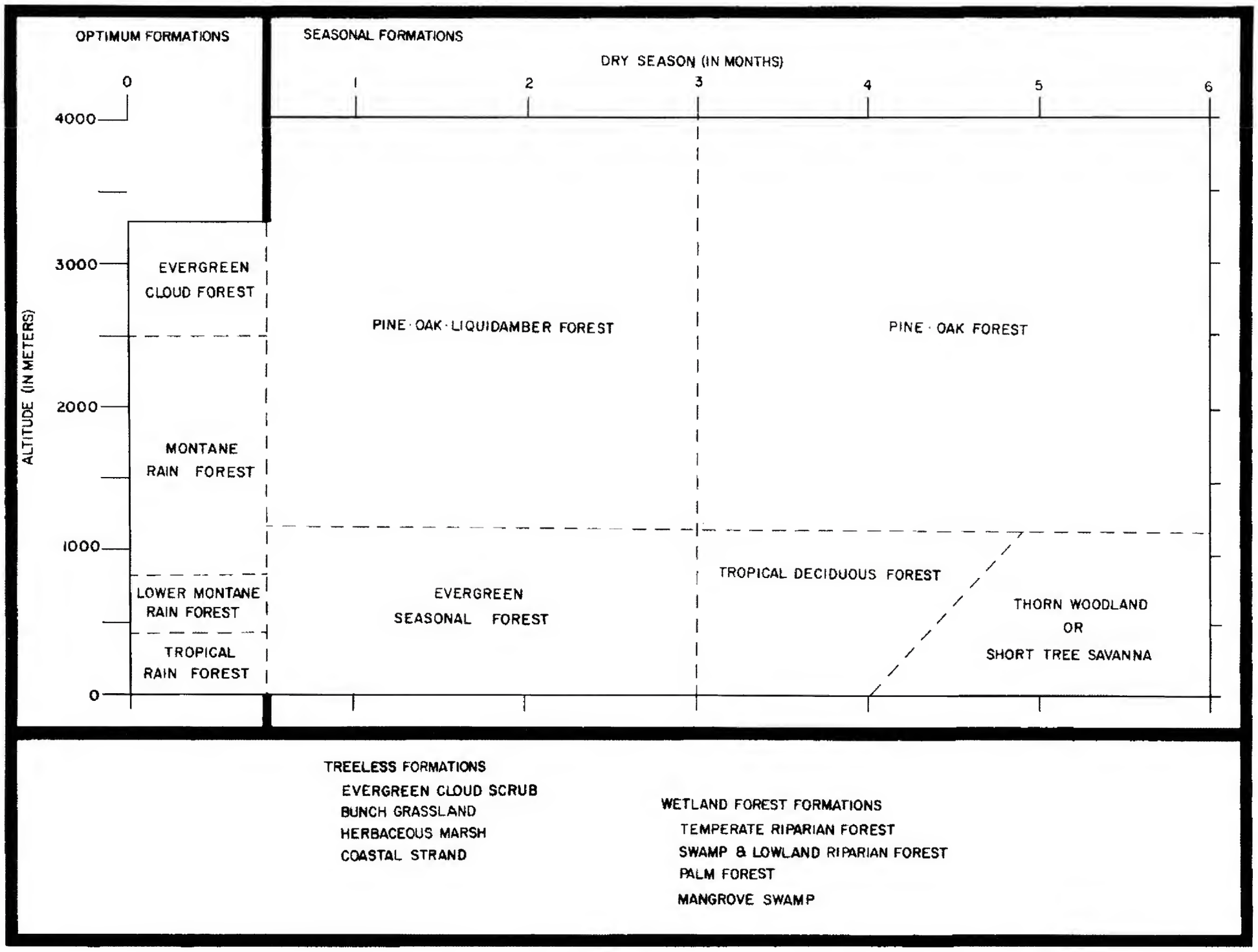


Figure 3.55. Plant formations of Chiapas, Mexico, and their altitudinal arrangement. From Breedlove (1973). Used with permission of the California Academy of Sciences, San Francisco.

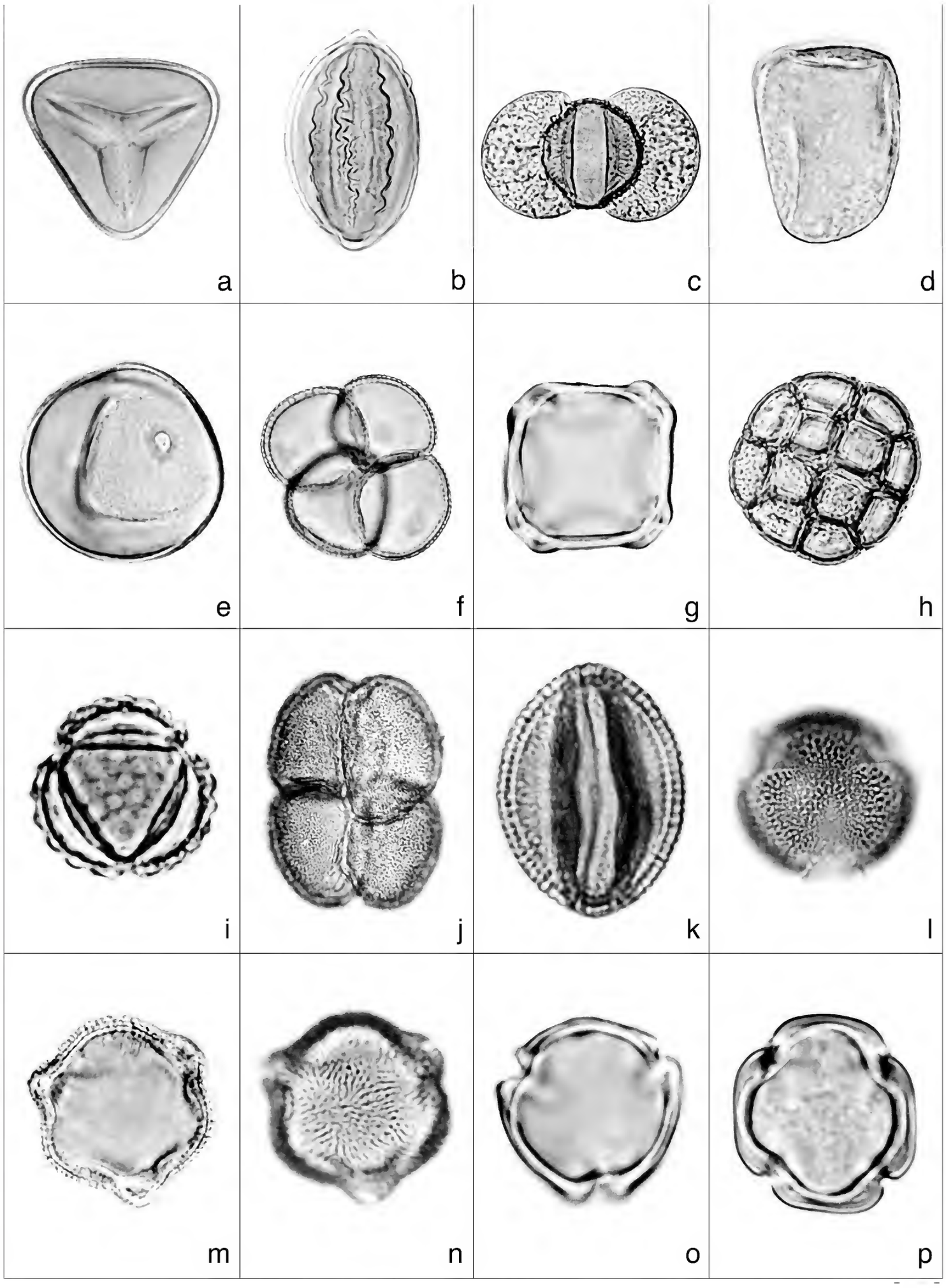


Figure 3.56. Modern spores and pollen from the vegetation of Mexico and northern Latin America. a = *Alsophila bicrenata*, b = *Ephedra*, c = *Podocarpus macrophylla*, d = Cyperaceae, e = Poaceae, f = *Typha latifolia*, g = *Alnus*, h = *Acacia*, i = *Ambrosia*, j = *Annona cherimelia*, k, l = *Avicennia germinans* (equatorial and polar views), m, n = *Bursera* (polar views, equatorial outline and surface), o = *Byrsonima crassifolia*, p = *Cedrela mexicana*.

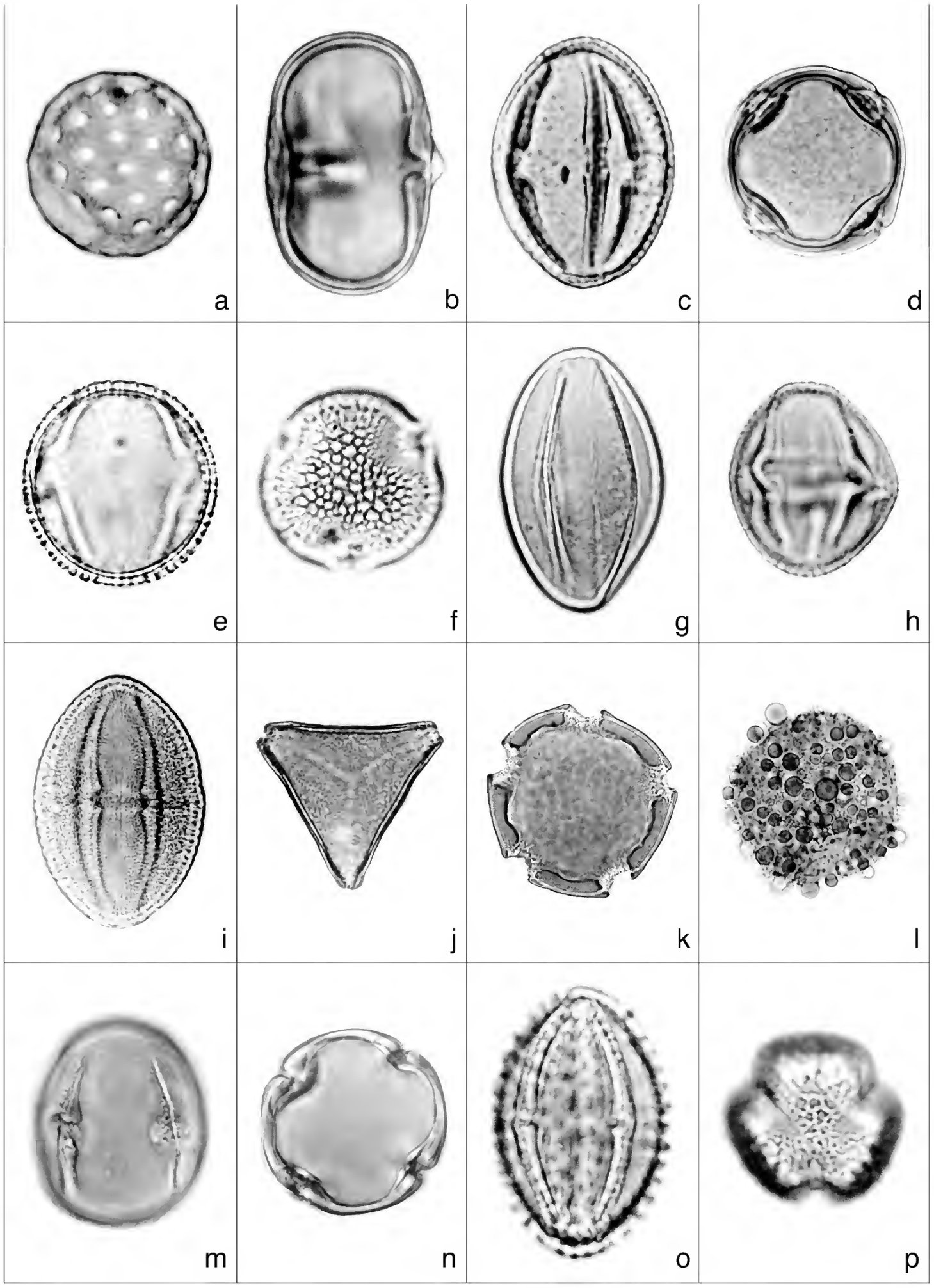


Figure 3.57. Modern spores and pollen from the vegetation of Mexico and northern Latin America. a = chenoam, b = *Chrysophyllum glabrum*, c = *Erythroxylum deciduum*, d = *Guarea chichon*, e, f = *Parkinsonia aculeata* (equatorial and polar views), g = *Prosopis juliflora*, h = *Rhizophora mangle*, i = *Sapium*, j = *Serjania cornigera*, k = *Symphonia globulifera*, l = *Tournefortia hirsutissima*, m, n = *Trichilia hirta* (equatorial and polar views), o, p = *Zanthoxylum clava-herculis* (equatorial and polar views).

THE ANTILLES

Our knowledge of the vegetation of the Antilles is based in considerable part on the monumental efforts of the myopic-of-purpose, maniacal-in-intensity, admirable eccentric, Swedish botanist Erik Ekman (1928), whose collections formed the basis for the nine-volume *Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis* by Ignatius Urban (1898–1928). Ekman traveled mostly by foot on physically demanding trips into remote areas, lived in poverty, and was perpetually undernourished, often ill, indifferent to his physical appearance, and uniquely asocial. After one exhausting trip, he fell asleep on the porch of a hut in Jacmel, Haiti, in a particularly disheveled state. He was awakened by a visitor prodding him with his foot and saying to a friend, "May I present Dr. Erik Leonard Ekman, member of the Swedish Royal Academy of Sciences, Fellow of the Smithsonian Institution, and the world's greatest authority on the Caribbean flora" (Roger Lundin, pers. comm., 2002).

Another important collection was made by Sir Hans Sloane in Jamaica between 1687 and 1689 while he was physician to the governor of the island, the Duke of Albemarle. There is a Flora of the Lesser Antilles (Howard, 1974 et seq.), a bibliography and Web site of Caribbean botany (Zanoni et al., 1984; Zanoni & Buck, 2005), the Flora of the Greater Antilles Newsletter (available at the New York Botanical Garden Web site at http://www.nybg.org/bsci/fga),[5] and reviews of the biogeography (Woods & Sergile, 2001) and historical biogeography and phylogenetics of Caribbean plants (Santiago-Valentin & Olmstead, 2004).

Only the most general of estimates can be given for the number of vascular plant species in the Antilles, but it is probably >10,000 based on Adams (1972, p. 9) and the data provided in Table 3.4. The principal systems for classifying the plant communities are those of Beard (1944, 1949, 1955), Stehlé (1945, 1946; Lesser Antilles), a modification of these by Howard (1973, 1974; Table 3.5), and Borhidi (1996; Appendix 1.4; names not in TROPICOS [MO] are from Howard [1973] and Borhidi [1996]).

The composition and arrangement of the vegetation are a result of an immensely complex set of interrelated factors, but they include the geographic isolation of the islands from continental landmasses since the Cretaceous and from each other for most of the Tertiary; the small area of many of the islands; and the insular environment that precludes such climatically important and biologically relevant factors as continentality, provides high atmospheric humidity throughout the year, and mitigates against excessively low evapotranspiration potentials. The driest habitats and the most arid vegetation within zones of low to moderate seasonal rainfall are a consequence of edaphic factors and location on the lee south-facing slopes of the central cordilleras and at the western end of the islands. Soils of low water-holding capacity resulting from the high porosity of coarse limestone substrates, or serpentine soils and coastal salt flats involving chemical desiccation, create physiologically dry conditions. The driest near-desert areas are south of the Sierra Maestra in Cuba, on the south sides of Puerto Rico and Hispaniola, and on the northwestern peninsula and Gonâve Island of Haiti. There are cacti (*Cephalocereus royeni*, *Leptocereus quadricostatus*, *Melocactus acunae*, *Ritterocereus hystrix*) associated with other xerophytic succulents such as *Agave missionum* and *Pedilanthus angustifolius*. Variation in rainfall has a marked effect on the vegetation, and the moisture-laden northeast trade winds produce wet to mesic forests on the windward north-facing slopes and at the eastern ends of the islands (Trejo-Torres & Ackerman, 2002).

Serpentine and bauxite—These minerals are widely distributed in the Greater Antilles and are an important part of the ecology. Serpentine is a group of silicate minerals oriented in layers or sheets (asbestos is an example) with the chemical formula $Mg_6[Si_4O_{10}](OH)_8$ (O'Hanley, 1996). Upon weathering, an excess of magnesium is released to the soil that, along with its low water-holding capacity and the seasonal rainfall, produces arid habitats supporting a low, dense, dry vegetation often characterized by high endemism (Cedeño-Maldonado & Breckon, 1996). Serpentine vegetation can be near desert in aspect, even in areas of moderate rainfall, but in general, MAP and evaporation from the ocean provide too much moisture for desert vegetation as typically defined. In the classification followed in this text, the cacti and other succulents in arid habitats and on serpentine soils are included as near-desert phases of the shrubland/chaparral–woodland–savanna formation (see Fig. 3.73, Puerto Rico).

Another distinctive mineral substrate in the Antilles, especially on Jamaica, is bauxite (from Les Baux de Provence in southern France). It is a complex mixture of up to three forms of aluminum hydrate (gibbsite, diaspore, and boehmite) concentrated through the weathering of rocks containing aluminium in tropical climates with high rainfall. There are often impurities of iron, phosphorus, and titanium, and depending on the amounts of these elements, bauxite soils may be nearly white, grey, yellow, brown, or red. Where iron is part of the residue, the red soil is called laterite. Where the residue contains 25%–30% or more of aluminium oxide, it is a com-

Table 3.4. Estimated number of vascular plant species in the Greater Antilles. From Figueroa Colón (1996).

Island	Area ($km^2 \times 1000$)	Species	Endemic (%)	Source
Cuba	114.9	6375	49.9	Borhidi (1996)
Jamaica	10.9	3003	26.1	Toledo (1985)
Hispaniola	76.2	5000	36.0	Toledo (1985)
Puerto Rico	8.9	2410	9.9	Liogier & Martorell (1982)

mercial source of aluminium ore (Allaby & Allaby, 1999). The largest deposits are in Australia and Brazil, but Jamaica has significant quantities of bauxite that have been mined extensively, and bauxite soils are one of the characteristic edaphic features of the island.

It might be expected that the vegetation on this chemically distinctive soil would be unique. The characteristics of bauxite soil most relevant to vegetation are that it is sterile, heavy (composed mostly of clay-size particles), has a high water-holding capacity, and is rich in aluminium oxide. Plants on these soils are often slow-growing with contorted stems, and show a browning or drying of the roots and root hairs in response to toxic levels of aluminium that cause poorly developed root systems. Like serpentine, it likely requires some physiological adaptation by plants to survive on this substrate. However, unlike serpentine, which often supports highly endemic and arid vegetation, the vegetation on bauxite soils in Jamaica is similar to that of the surrounding communities, and studies by Aspery and Robbins (1953; Howard & Proctor, 1957a, b) failed to find any specific relationship between the vegetation and these soils. Among the trees that probably grew originally on the now highly disturbed bauxite substrates are *Cedrela odorata*, *Ceiba pentandra*, *Coccoloba plumieri*, *C. swartzii*, *Dipholis nigra*, *Swietenia mahagoni*, and *Terminalia latifolia*, and all these occur elsewhere on the island (see Appendix 1.6).

The most extensive potential natural community over much of the Antillean landscape is shrubland/chaparral–woodland–savanna growing in dry habitats to the lee of mountains, on south-facing slopes, on the western end of the larger western islands, and on coarse porous or serpentine soil. The prominence of this formation at present, however, is due to increasing aridification associated with human activity. Chaparral (thorn scrub) is widespread and consists of plants known from similar habitats throughout northern Latin America, including *Acacia*, *Acidoton*, *Brya*, *Bursera*, *Calliandra*, *Cereus*, *Croton*, *Guettarda*, *Haematoxylum*, *Jatropha*, *Opuntia*, *Phyllanthus*, *Pictetia*, *Piscidia*, *Pithecellobium*, *Psychotria*, *Rauvolfia*, *Rondeletia*, *Tabernaemontana*, and *Tabebuia*. Natural dry savannas uninfluenced by anthropogenic factors are not presently known in the Antilles, but highly modified remnants may occur on Isla de la Juventud and in the Pinar del Río Province of mainland Cuba. In the Villa Clara Province of Cuba, there are grasslands underlain by serpentine that support scattered trees of *Acacia*, *Bursera*, *Byrsonima*, *Curatella*, *Erythroxylum*, *Jacaranda*, and *Rondeletia*; in the Lesser Antilles (e.g., on Antigua), there are grasslands with *Prosopis* (mesquite); and the Grand Savanna of Dominica consists of trees of *Byrsonima* and *Haematoxylum* with an understory of the grass *Sporobolus*. From this complex of shrubland/chaparral–woodland–savanna vegetation, *Acacia*, *Bursera*, Poaceae, and *Jacaranda* have been reported from the fossil record of the Antilles, but these genera extend into other vegetation types.

Natural grasslands are not extensive in the Antilles. On rocky peaks where the soil is thin (e.g., El Yunque, Puerto Rico), there are grassy areas; however, most communities in which grasses are prominent either have scattered trees and qualify as disturbed, highly modified savannas, or their extent is primarily a consequence of agriculture, burning, or overgrazing.

Table 3.5. Classification of the vegetation types of the Antilles used by Howard (1973).

COASTAL FORMATIONS			
beach	strand	rock pavement	mangrove
LOWLAND FORMATIONS			
thorn scrub	savanna	marsh or swamp	alluvium
MONTANE FORMATIONS			
wet or dry forests on limestone		montane sclerophyll	
palm brakes		tree fern communities	
pine forests		cloud forests	
volcanic and soufrière communities		crater lakes	
elfin thickets			

There are mangrove, beach/strand/dune, freshwater herbaceous marsh/swamp/bog, and aquatic communities in the Antilles. The mangrove formation includes genera frequent throughout Latin America—*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, and *Rhizophora mangle*, commonly associated with *Acrostichum*, *Caesalpinia*, *Dalbergia*, *Drepanocarpus* (*Machaerium*), *Hibiscus*, *Malache* (*Pavonia*), *Piscidia*, *Pterocarpus*, and *Ximenia*. As noted previously, the mangroves occupy habitats ideally suited for preservation of plant microfossils, and the record from the Antilles includes *Rhizophora* pollen and *Acrostichum*-type spores. In addition, *Pelliceria*, a mangrove presently distributed from the Caribbean coast of Nicaragua (Roth & Grijalva, 1991) through southern Central America to northwestern Colombia, was present in the Antilles and Mexico until at least the middle Oligocene, and *Caesalpinia*, *Hampea–Hibiscus*, and *Laguncularia* are known from other Cenozoic deposits in adjacent Mexico and Central America.

The beach/strand/dune vegetation consists of a cadre of plants frequent along the coasts of Latin America, including the grasses *Distichilis*, *Sporobolus*, and *Uniola*; *Batis*, *Canavalia*, *Cenchrus*, *Coccoloba uvifera* (sea grape), *Conocarpus*, *Euphorbia*, *Ipomoea*, *Pilocereus* (*Cephalocereus*), and *Sesuvium*. Inland on stabilized substrate, there are many equally widespread strand plants such as *Bontia*, *Caesalpinia* (*Guilandina*), *Chrysobalanus*, *Erithalis*, *Hippomane*, *Metopium*, *Scaevola*, *Suriana maritima*, *Terminalia amazonia*, and *Tournefortia*. Where coral/algal limestone is exposed, it weathers into soft and porous material, or it may be hard and consolidated, and mineral limestone often weathers into a surface with sharp points called dogtooth limestone (Howard & Briggs, 1953). Collectively, these substrates are known as rock pavement, and they support such plants as *Achyranthes*, *Catesbaea*, *Cnidoscolus*, *Colubrina*, *Comocladia*, *Cordia*, *Dodonaea*, *Ernodea*, *Eugenia*, *Guettarda*, *Gymnanthes*, *Jacquinia*, *Lantana*, *Melocactus*, *Pectis*, *Phyllanthus*, *Phyllostylon*, *Portulaca*, *Rachicallis*, *Randia*, *Reynosia*, *Sesuvium*, *Strumpfia*, *Swietenia*, *Tabebuia*, and *Victoria*. Alluvium (river silt) communities include the endemic cycad *Microcycas*,

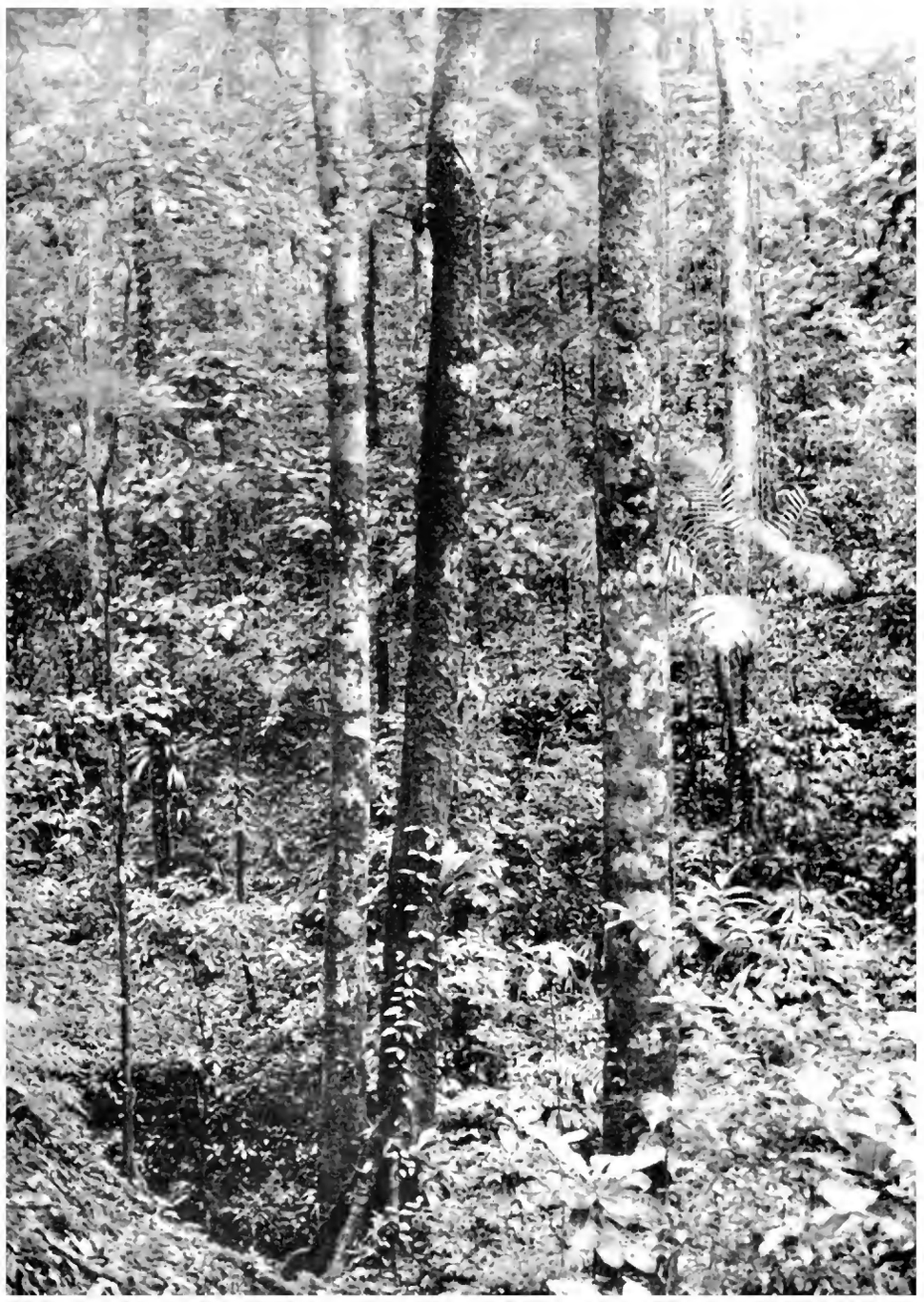


Figure 3.58. Rain forest/montane wet forest (wet phase of lower to upper montane broad-leaved forest) on Grenada, Lesser Antilles. The buttressed tree in the foreground is *Sloanea berteroana*, and the two trees immediately behind are *Dacryodes excelsa*. From Beard (1949). Used with permission of Oxford Forestry Institute.

Bejaria, *Kalmia*, *Lachnocaulon*, *Lechea*, *Pieris*, and *Quercus*, and another cycad, *Zamia*, grows in coastal thickets and woodlands. Specialized communities occur where salt outcrops or where the substrate periodically dries out to produce other evaporites, and are composed of *Achyranthes*, *Annona*, *Atriplex*, *Batis*, *Capparis*, *Heliotropium*, *Pithecellobium*, *Salicornia*, *Suaeda*, and *Thespesia*. All these phases are included here in the beach/strand/dune formation.

The opportunities for preservation of these communities are limited and, with the exception of *Eugenia* type, Poaceae, *Tournefortia*, and some chenoam pollen possibly representing *Atriplex* or *Suaeda*, the formation is poorly represented in the fossil record of the Antilles.

The largest freshwater herbaceous marsh/swamp formation (with some woody associates) in the Antilles is Ciénaga de Zapata on the south coast of Cuba (one part is familiar as the Bahía de Cochinos or Bay of Pigs). Another is in the eastern Dominican Republic near Higüey, while similar habitats are found along the margins of the several crater lakes in the Antilles. Prominent plants are *Acoelorraphe*, *Cladium* (saw grass), *Coccothrinax*, *Eleocharis*, *Fraxinus*, *Gerardia*, *Polygonum*, *Rhynchospora*, *Sabal* (palmetto palm), *Sagittaria*, *Solidago*, *Typha*, *Valisneria*, and *Vicia*. There are small hillside seepages in the Luquillo Mountains of Puerto Rico that support marsh or bog plants familiar in northern North America such as *Ascyrum*, *Drosera* (sundew), *Lobelia*, *Potentilla*, *Sisyrinchium*, *Stellaria*, *Utricularia*, *Viola*, and *Xyris*. Aquatics include *Nuphar*, *Nymphaea* (water lily), and *Pistia stratiotes*. Other than Poaceae, none of the above genera have been reported from the fossil record of the Antilles.

The lowland Neotropical rain forest is absent or poorly developed in the Antilles because even in the wettest habitats, the rainfall is too seasonal or run-off is too rapid to support the community. Odum (1970) argues that the *Dacryodes excelsa* (tabonuco)–*Sloanea berteroana* forest on the slopes of El Verde in the Luquillo Mountains of Puerto Rico is a rain forest, but others (Holdridge, 1970, pp. B28–B30) consider it a montane wet forest. On a local scale, it is probably not of great importance whether a vegetation type on Cuba or Puerto Rico is considered lowland Neotropical rain forest or the wettest association within the lower to upper montane broad-leaved forest. However, if in a broader treatment these formations are to be compared with those in Amazonia and elsewhere;

Figure 3.59. Rain forest/montane wet forest (wet phase of lower to upper montane broad-leaved forest) on St. Kitts, Lesser Antilles. The large buttressed tree in the foreground is *Sloanea berteroana*. The other trees are the palm *Euterpe globosa*. From Beard (1949). Used with permission of Oxford Forestry Institute.

if their presence is to be sought among fossil assemblages; and if paleoenvironmental reconstructions are to be based on their presence or absence, then a consistent definition of the formation is desirable. In the present treatment, the lowland Neotropical rain forest is the narrowly defined community, recognized on the basis of features previously discussed for Veracruz and later for Amazonia, while transitions are included in the low-elevation, wet associations of the more broadly defined lower to upper montane broad-leaved forest. Examples of the *Dacryodes–Sloanea* forests of the Antilles (Grenada, St. Kitts) are shown in Figs. 3.58 and 3.59.

The lower to upper montane broad-leaved forest formation has several associations defined by the availability of moisture (MAP, slope and drainage, lee or windward exposure, seasonality), successional stage, and substrate. The present agricultural lowlands immediately behind the mangroves and beach/strand/dune vegetation were probably formerly occupied by a fringe of lowland tropical rain forest. Certainly the climates are suitable. A rain gauge installed at Hacienda La Perla (elevation 140 m) in the northeastern foothills of the Luquillo Mountains of Puerto Rico in 1897 recorded an average MAP of 3120 mm for each of the following two years, and the number of rainy days was recorded as "nearly 300 per year" (Wadsworth, 1970). MAT in the lowlands is 25° C. There are few remnants, however, and the plant fossil record is equivocal about the former presence of lowland tropical rain forest in the Greater Antilles.

Beginning inland at ~150 m on the north-facing slopes, MAP increases and at La Mina, Puerto Rico (elevation 720 m), in some years, rainfall is as high as 4650 mm. The wettest areas support the tallest trees (~30–35 m) of the lower to upper montane broad-leaved forest formation, which in the Holdridge (1970) system is designated as the subtropical wet forest-subtropical lower montane wet forest. Its greatest extent is the El Verde forest in the Luquillo Mountains on the north side of Puerto Rico (Odum, 1970), where *Dacryodes excelsa* (tabonuco) and *Sloanea berteroana* are prominent components. This community will be discussed further under the vegetation of Puerto Rico. Comparable associations are *Dacryodes–Sloanea* on Dominica (Beard, 1949), Puerto Rico (Dansereau, 1966), and Guadeloupe (Stehlé, 1945); *Sloanea berteroana–Ormosia krugii* on Hispaniola (Ciferri, 1936); *Psidium montanum–Calophyllum jacquinii* on Jamaica (Aspery & Robbins, 1953); and *Carapa guianensis* forests on Cuba (Borhidi, 1996).

At places farther upslope, the forest is reduced in stature to 12–15 m, fog is frequent, and mosses and other epiphytes are common. This is the mossy or cloud forest association (Silver et al., 2001), and it includes *Charianthus*, *Clusia*, *Cyrilla racemiflora* (Colorado tree), *Didymopanax*, *Eugenia*, *Freziera*, *Hibiscus*, *Ilex*, *Inga*, *Miconia*, *Ocotea*, *Oreopanax*, *Psychotria*, *Richeria*, *Tabebuia*, and *Weinmannia*. Above the zone of clouds, it is drier, winds on the peaks frequently reach 100 km/hr, and the trees are low and twisted to form an elfin forest. Nearly pure stands of the tree fern *Cyathea arborea* and the palms *Prestoea montana* or *Euterpe globosa* (sierra palm) occur locally within the lower to upper montane broad-leaved forest formation as successional or edaphic phases.

Figure 3.60. Coniferous forest of *Pinus occidentalis* near the summit of Pico Duarte, Dominican Republic. Photograph by William Buck.

The drier associations of the lower to upper montane broad-leaved formation grade into the shrubland/chaparral–woodland–savanna formation, and they often occur on outcrops of dogtooth limestone, on the characteristic erosion-produced mogotes or haystack mountains on Cuba and Puerto Rico, and in the cockpit country of Jamaica. These hills are steep-sided and porous, with numerous caverns, and often support a number of endemic taxa—e.g., *Bombax emarginatum* and *Gaussia princeps* on Cuba and western Puerto Rico; *Spathelia* on Cuba, Jamaica, and the Bahamas. Other more widespread genera are *Alchornea*, *Amyris balsamifera* (sandalwood), *Andira*, *Bucida*, *Buchenavia*, *Calophyllum*, *Dendropanax*, *Dipholis*, *Elaphrium*, *Ficus*, *Guaiacum officinale* (lignum vitae), *Mammea*, *Oxandra*, *Psidium*, *Sapium*, and *Zanthoxylum flavum* (satinwood). One difference between the lower to upper montane broad-leaved forest of the Antilles, and that of Mexico and northern Central America, is the fewer number of temperate elements of northern affinities. Some do occur (e.g., *Juniperus*, *Pinus*, *Celtis*, *Fraxinus*, *Ilex*, *Juglans*, *Magnolia*, *Myrica*, *Prunus*, *Quercus*, *Salix*), but many characteristic genera are absent even at the highest elevations (e.g., *Abies*, *Picea*, *Carpinus*, *Cornus*, *Fagus*, *Liquidam-*

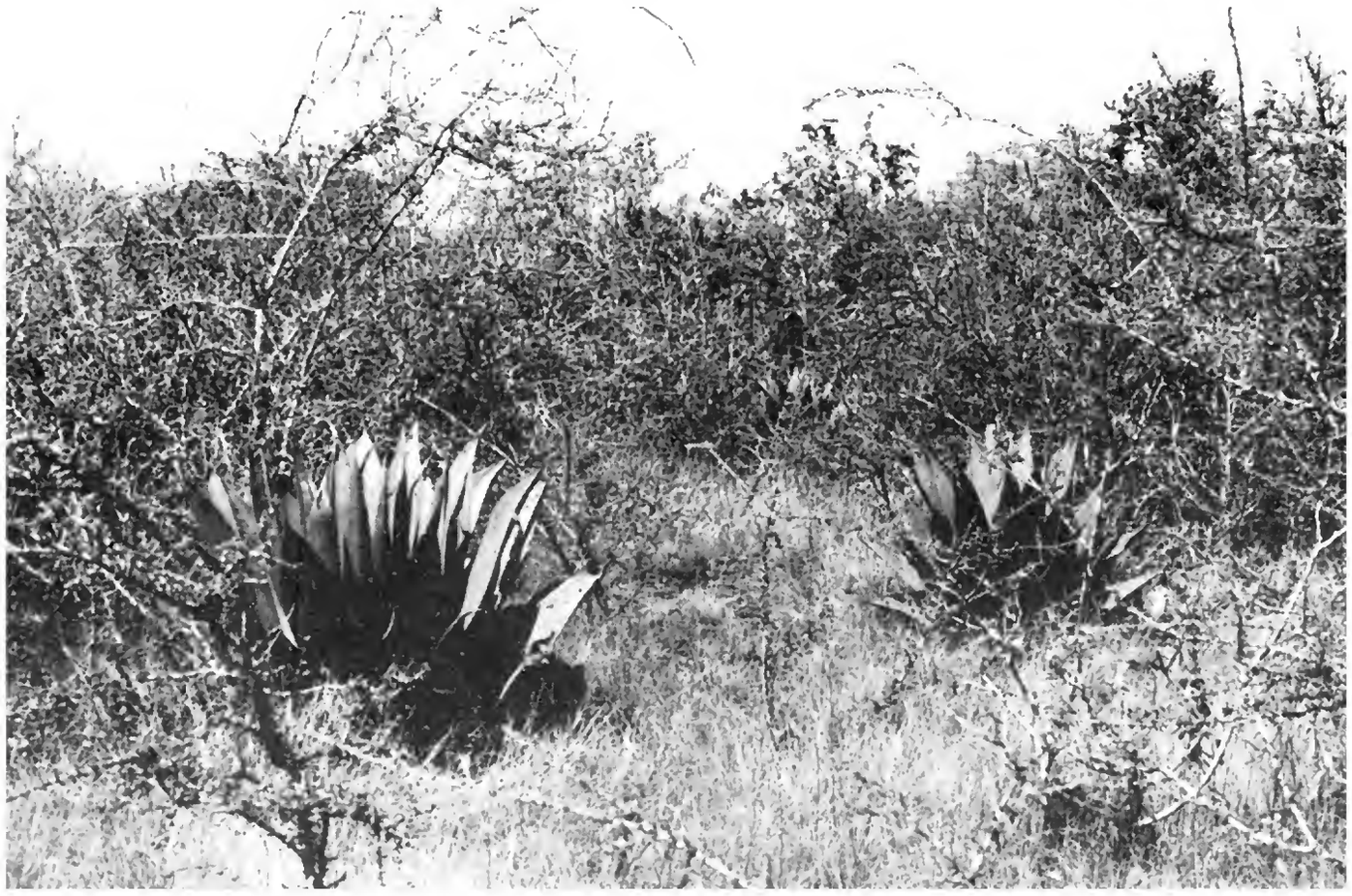


Figure 3.61. Thorn scrub woodland on serpentine, Santa Clara Province, Cuba. Plants include *Brya ebenus*, *Erythroxylum minutifolium*, and *Agave brittoniana*. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

bar, *Nyssa*, *Ostrya*, *Tilia*, *Ulmus*). The lower to upper montane broad-leaved forest formation is one of the principal paleocommunities represented in the mid to late Cenozoic record of northern Latin America, and fossil pollen reported from the relatively few paleofloras of the Greater Antilles include *Cyathea*, Arecaceae, *Dendropanax*, *Eugenia* type, *Guarea*, *Ilex*, and *Pleodendron*.

Coniferous forests of *Pinus* (*P. caribaea*, *P. cubensis*, *P. tropicalis*) grow on Cuba, particularly western Cuba and on Isla de la Juventud, now mostly as highly modified savanna-like communities. The endemic *Pinus occidentalis* is the dominant pine on Hispaniola forming pine woods, mixed in cloud forests between 1000 and 2340 m elevation (Judd, 1987), and it is the principal tree at the summit of Pico Duarte (Fig. 3.60). The easternmost distribution of *Quercus* in the Antilles is on Cuba, represented by the evergreen oaks *Q. oleoides* and *Q. sagraeana*. They grow both with and separate from the pines, but where they are separate, many of the associated species of trees, shrubs, and herbs are the same, and in earlier times pine-oak woodlands were probably more extensive on Cuba. Elsewhere, for example, allozyme analyses of a 180-ha isolated stand of *Pinus caribaea* var. *hondurensis* near Tikal, Guatemala, suggest it is a relic of a once widespread and more continuous population, probably when climates were drier, rather than a former plantation of the Maya (Dvorak et al., 2005). Pollen of *Pinus* has been reported from the Tertiary and Quaternary of the Greater Antilles, but *Quercus* is presently unknown from both the mega- and microfossil record.

Most of the land in the Antilles is below 1000 m, and the highest summits (e.g., Pico Duarte, Dominican Republic, 3175 m; Pico Turquino [Real], Cuba, 1974 m; El Yunque, Puerto Rico, 1077 m) are too low and the MAT is too high to support alpine tundra (páramo). The rock vegetation with low shrubs of *Machaerina restioides* growing among mats of mosses on El Yunque, Puerto Rico, is similar in structure to páramo, but the environmental conditions are different. Borhidi (1996) considers the vegetation on the highest peaks of Cuba an evergreen subalpine shrub woodland, and on Pico Duarte it is montane coniferous forest (*Pinus occidentalis*).

Endemism and the Caribbean Hot Spot—Endemism is the restriction of a taxon to a specific and often limited geographic region. It is a noteworthy feature of many environmentally diverse and/or geographically fragmented areas, such as islands, mountain peaks and tepuis, distinctive soils (e.g., serpentine) or soil types surrounded by ones of different composition, and extreme environments such as deserts surrounded by more mesic habitats (viz., Mexico, Rzedowski, 1973; Brazil, caatingas and cerrado, Novaes Pinto, 1994). The number of single-island endemics in the Antilles is estimated at 6550 species and 205 genera (cf. the National Museum of Natural History Web site at http://www.nmnh.si.edu/botany/projects/cpd/ma/ma-carib.htm). Endemism is extensive on Cuba for which Borhidi (1996, p. 216) lists 3178 endemic plant taxa constituting 49.9% of the actual flora and 53% of the native flora, and Howard (1973, p. 25) lists 40 genera of plants found only on Cuba. There are ~3304 species of vascular plants reported from Jamaica, and 923 (27.9%) are endemic. In Jamaica, there is a proposal to make Dolphin Head Hills in the northwest part of the island a national park, in part because of its unique flora. It is a limestone outcrop isolated by shale on three sides and an alluvial plain on the other. Although only ~1300 ha in size, it is an example of extreme endemism with 451 known species of vascular plants of which 130 are restricted to Jamaica and 21 to Dolphin Head Hills.

Among the complex of factors causing endemism is the geographic and consequent reproductive isolation of individuals from the parent population. Each surviving isolated population is unlikely to have the full genetic complement of the parent population, and it is equally unlikely that they will be identical to one another. Natural selection acting on these

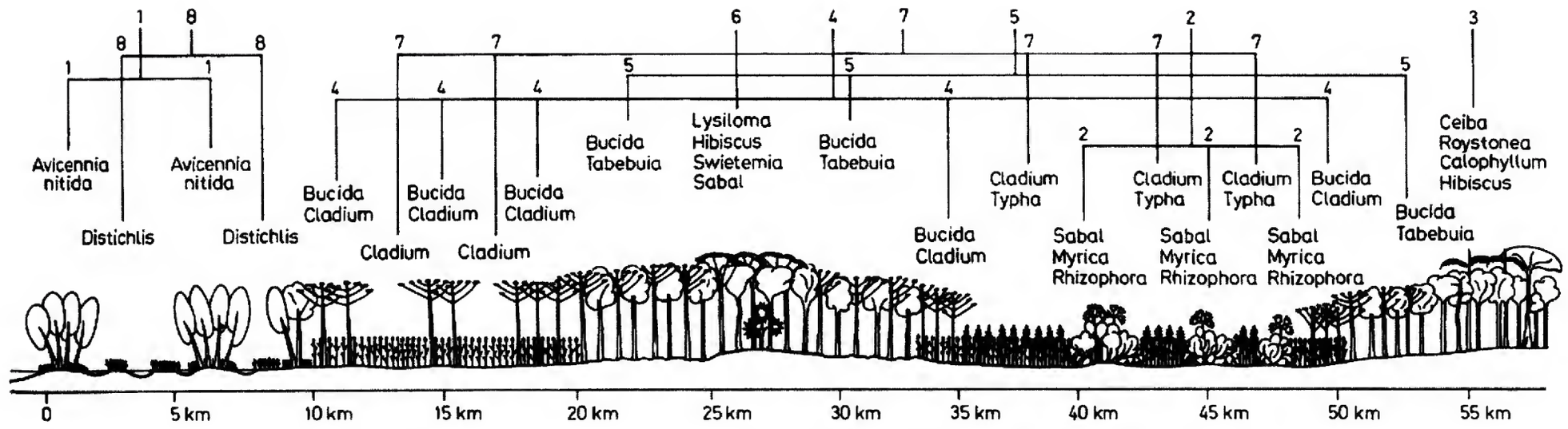


Figure 3.62. Vegetation transect through the western basin of the Zapata Swamp. 1 = mangrove, high salinity; 2 = mangrove, low salinity; 3 = tropical evergreen seasonal forest; 4 = swamp forest on peat; 5 = swamp forest on limestone; 6 = tropical semi-deciduous forest; 7 = herbaceous swamp; 8 = saline herbaceous swamp. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

isolates can produce phenotypically distinct populations of local distribution.

Endemism can be used to assess the likely naturalness or the anthropogenic origin of vegetation. For example, it is often difficult to determine if comparatively small areas of grassland or savanna are relatively old and natural, or more recent and a product of human activity. Endemics would most often predate human presence and offer a clue. Endemism may also reflect geologic history. For example, according to Borhidi (1996, pp. 286–287), 30 endemic genera of vascular plants are shared between Cuba and Hispaniola, which are known to have been connected and emergent in the middle Eocene (45 Ma). They were not separated until the early to middle Miocene (20–25 Ma) and are still only 72 km apart across the Windward Passage. In contrast, 10 endemic genera are shared between Cuba and Jamaica, which may never have been connected, with Jamaica re-emerging only in the late Miocene (10 Ma), and presently separated by ~160 km. The correspondence between geologic factors and patterns of endemism is most likely noticed when the broadly defined ecosystem perspective mentioned earlier is brought to the study of tropical vegetation. Among the many other factors likely involved in patterns of endemism in the Antilles are the directional atmospheric and ocean currents generated by the trade winds from the northeast.

It is evident that if environmental destruction is extensive in areas with high endemism, the extinction of species will be great because they occur nowhere else. At present, the Caribbean region is the Earth's third richest biologically and most endangered terrestrial ecosystem as defined by Conservation International.[1] It ranks even higher if southern Florida is excluded, because numerous non-endemic northern elements extend into Florida and dilute calculations of Caribbean endemism. The number of endemic plant species in the Greater and Lesser Antilles is estimated at 7000.

The spore and pollen signatures for the various plant formations of the Greater Antilles are similar to those discussed earlier for Mexico. There are no catalogs specifically for the Antilles, and modern pollen rain studies have been made only for the Dominican Republic (Chapter 5). Information on modern spores and pollen for some Antillean plants is included in the *Flora Neotropica* (NY).

In the following discussion, the vegetation of the principal islands is summarized because fossil floras are known from each of them, they have been separated since at least the Miocene, and each presents a unique aspect of Antillean vegetation. Cuba is the largest island with the most extensive flora. Its vegetation is described first and in most detail as representative of the Greater Antilles. Additional information is provided for the other islands to illustrate unique, extensive, especially well-preserved, or exceptionally well-studied floras; e.g., El Verde of Puerto Rico, the greatest extent of lower to upper montane broad-leaved forest on the islands, and the cloud forest–pine forest of La Visite and Pic Macaya National Parks of Haiti. When viewed collectively, these communities provide the background for later consideration of the past history of Antillean vegetation and its paleoenvironments.

Cuba

The vegetation of Cuba consists of ~7000 species of vascular plants. Early studies include those of Urban (1898–1928), León (1946), León and Alain (1951–1957), Alain (1962; supplement, 1969), Marie-Victorín and León (1942, 1944, 1956), and Howard and Briggs (1953) on the shrubland of the dogtooth limestone on the south coast of Las Villas. Vegetation maps include those of León (1946), Voronov (1970), and Borhidi and Muñiz in Borhidi (1996). In the older literature, the names of some collecting localities and political subdivisions differ from those used today because the provinces have been renamed. The two systems are shown in Fig. 1.13.

A recent summary of the vegetation is by Borhidi (1996). It includes a wealth of information on the composition of the communities, their distribution in Cuba, and the meteorological, ecological, and edaphic conditions under which they grow. An earlier analysis of endemism, geographic affinities, presumed pathways of migration, and vicariance-dispersal-speciation mechanisms dependent on a modern taxonomy was questioned by Beurton (1993).

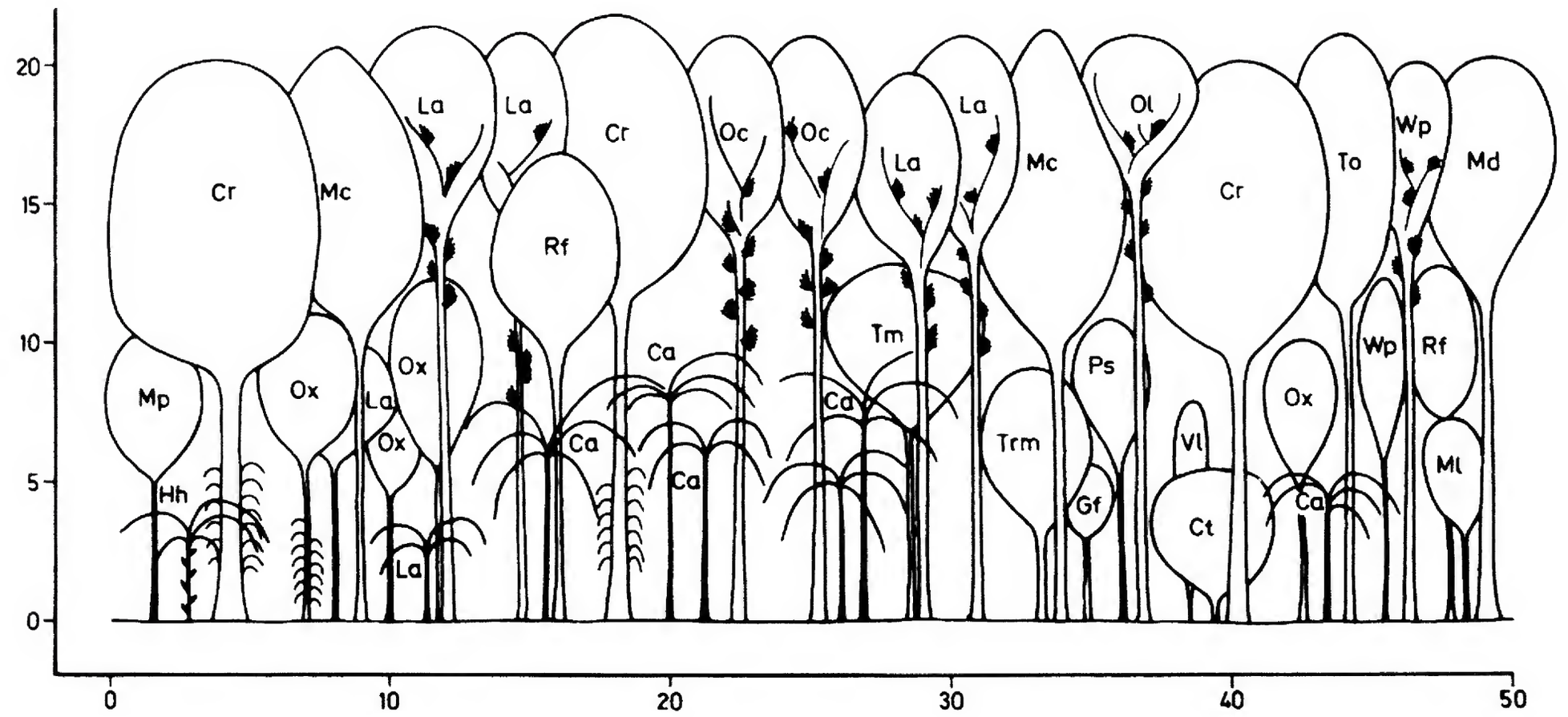


Figure 3.63. Profile of montane humid rain forest (wet phase, montane broad-leaved forest), Sierra Maestra (1350 m), Cuba. Ca = *Cyathea arborea*, *C.* sp.; Cr = *Cyrilla racemiflora*; Ct = *Clusia*; Gf = *Garrya fadyenii*; Hh = *Hemitelia horrida*; La = *Laplacea*; Mc = *Magnolia cubensis*; Md = *Matayba domingensis*; Ml = *Meriania leucantha*; Mp = *Miconia punctata*; Oc = *Ocotea cuneata*; Ox = *Oxyandra* (*Sloanea*) *laurifolia*; Ps = *Persea similis*; Rf = *Rapanea ferruginea*; Tm = *Talauma minor*; To = *Tabebuia oligolepis*; Trm = *Ternstroemia*; Vl = *Vaccinium leonis*; Wp = *Weinmannia pinnata*. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

About 75% of Cuba is covered by agricultural land or secondary vegetation. The least disturbed communities are confined mostly to mountainous regions too steep for cultivation or the gathering of wood for fire and charcoal, such as in the Sierra Maestra; salt or freshwater coastal marshes; or regions with substrate too dry or chemically unsuitable for agriculture (e.g., serpentine). Borhidi (1996) recognizes 11 potential natural vegetation types for Cuba, and these are incorporated into the system used here in Appendix 1.4.

The warmest and driest regions of Cuba are along the southeastern coast of the former Oriente Province in the rain shadow of the Sierra Maestra, where the MAT is 27°–28° C and the MAP is 350–500 mm. Although the MAP is low, every month has some rain and the high evapotranspiration potential is offset by the insular environment. In some locales, however, the effects of low rainfall are augmented by a porous limestone karst topography that supports shrubland or chaparral (Fig. 3.61) or by a coarse sandy soil that supports shrubland with succulent-Cactaceae phases (*Agave–Leptocereus*, *Pilocereus* [*Cephalocereus*], *Rhipsalis*, *Ritterocereus*, *Selenicereus*), shrubs (*Brya*), thorny shrubs (*Erythroxylum*), or trees with large water-holding capacity (*Bombacopsis*, *Gaussia*). In northeastern Cuba, the MAP is greater (950–1500 mm), but much of the substrate is coarse limestone and serpentine and the vegetation is still shrubland (evergreen woodlands, evergreen microphyllous, or semi-deciduous forest; Borhidi, 1996), while pine forests grow on latosols (high-mineral soils, often red from iron; viz., laterites). Among the prominent trees of this dry vegetation in the northeast are *Antirhea abbreviata*, *Byrsonima biflora*, *Clusia callosa*, *Coccoloba nervosa*, *Cyrilla cubensis*, *Garcinia polyneura*, *Ilex berteroi*, *Illicium cubense*, *Jacaranda arborea*, *Laplacea benitoensis*, *Lyonia glandulosa*, *Moacroton lanceolatus*, *Myrica shaferi*, *Rauvolfia salicifolia*, *Tapura cubensis*, and *Xylosma*.

Chaparral grows on the dogtooth limestone of Cuba, and it is a low (2–3 m), nearly impenetrable vegetation most extensively developed in the Oriente Province. The principal trees are *Ateramnus lucidus*, *Auerodendron cubense*, *Cassia emarginata*, *Colubrina elliptica*, *Cordia leucosebestena*, *Diospyros grisebachii*, *Erithalis fruticosa*, *Picrodendron macrocarpum*, *Polygala cuneata*, *Pseudocarpidium avicennioides*, *Spirotecoma spiralis*, and *Thouinia pseudopunctata*.

Dry deciduous woodlands are not extensively developed in Cuba because deciduousness at mid-elevations in the lower latitudes is primarily a response to seasonality in rainfall, and in Cuba even the most arid regions receive some rain in the dry season, along with moisture from the ocean throughout the year. Also, deciduousness, rather than being concentrated during a period of several weeks to a few months, is diffused over a longer season. The driest shrubland and woodland vegetation is described by Borhidi (1996) as semi-deciduous. The semi-deciduous xerophytic forests of east-central Cuba are 12–15 m in height, MAP is 800–1200 mm, and the driest season may be up to six months long. Among the prominent trees are *Ateleia apetala*, *Belairia spinosa*, *Bursera simaruba*, *Canella winterana*, *Carpodiptera cubensis*, *Copernicia baileyana*, *Cordia collococca*, *Diospyros halesioides*, *Gossypiospermum praecox*, *Manilkara jaimiqui*, *Maytenus buxifolia*, *Phyllostylon brasiliense*, *Pisonia*, and *Tabebuia anisophylla*.

Savannas are highly modified communities in Cuba that may be subdivided into an almost infinite number of phases depending on edaphic conditions, depth of the water table, degree of disturbance, or which particular trees or shrubs are left

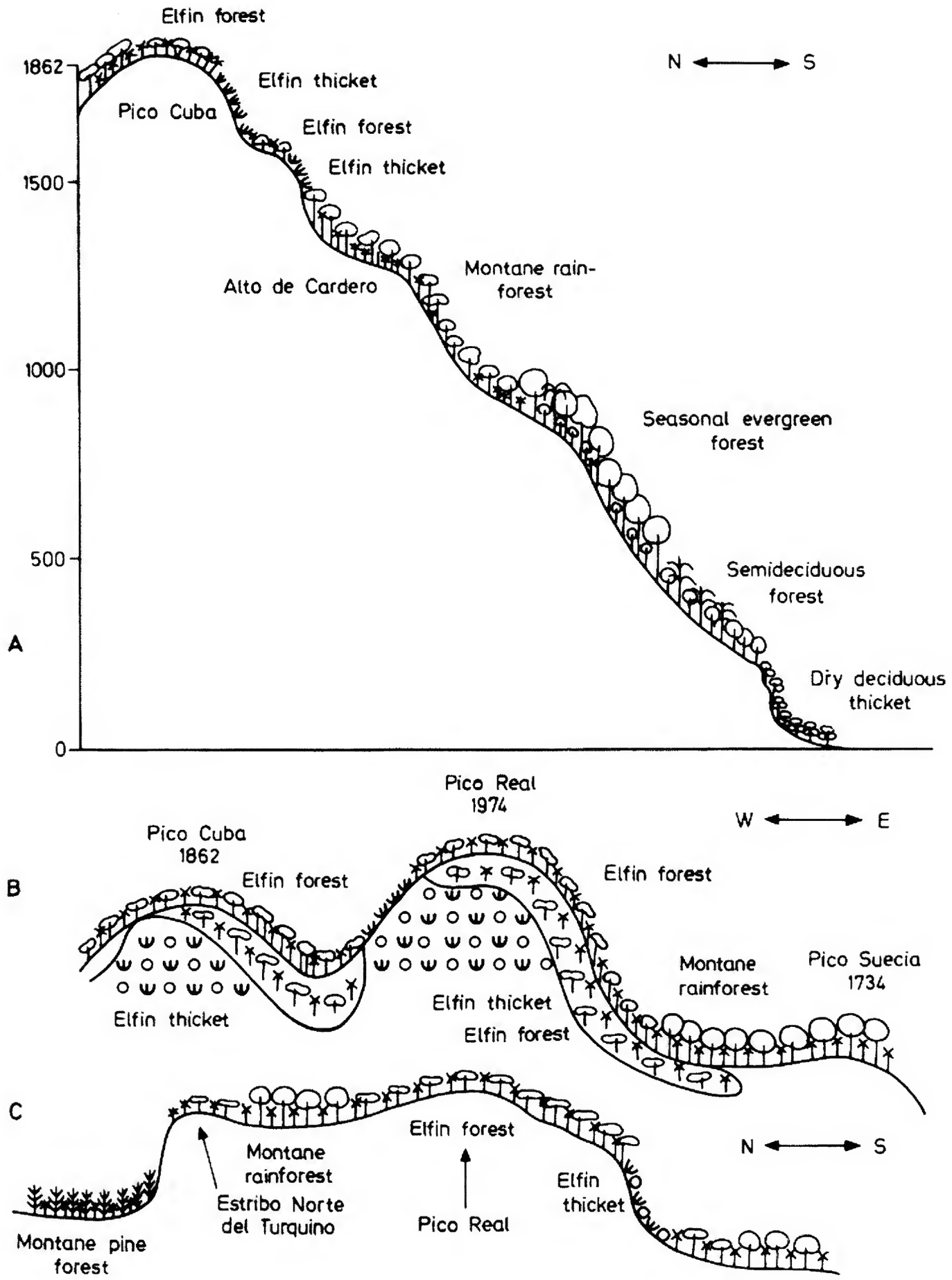


Figure 3.64. Vegetation transect through the high-altitude vegetation zones of Pico Turquino, Cuba. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

standing when the land is cleared (e.g., *Ceiba pentandra*). There are tall palm (*Sabal parviflora*, *Roystonea regia*)–tall grass and small palm (*Coccothrinax miraguama*, *Copernicia glabrescens*)–dwarf grass phases, the extent, if not the origin, of which result from selective preservation of these economically important plants. There are also grasslands with scattered *Pinus*, *Byrsonima*, *Erythroxylum*, *Jacaranda*, or *Rondeletia*, but many of these trees and shrubs are also components of the shrubland/chaparral–woodland, pine forest, or even rain forest vegetation (e.g., *Ceiba pentandra*). It is likely that members of the savanna-like communities are remnants of these formations.

As noted previously, the shrubland/chaparral–woodland–savanna environment is not suitable for the preservation of plants. From the dry-habitat associations described above, fossil pollen of *Bursera*, *Ilex*, *Jacaranda*, *Rauvolfia*, and some Poaceae, Arecaceae, and chenoams known from the Tertiary of the Antilles may represent this formation.

Mangrove vegetation is composed of plants widespread in the Caribbean region and in most of the tropical coastal regions of the world. The principal plants are *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, and *Rhizophora mangle*, associated with *Acrostichum aureum*. A transect through the western basin of the Zapata Swamp in Matanzas Province, southern coastal Cuba, is shown in Fig. 3.62. *Acrostichum*-like

Figure 3.65. Mossy forest, Pico Real, Turquino Mountains (1900 m), Cuba. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

spores and pollen of *Pelliceria* and *Rhizophora* are known from the Cenozoic of the Greater Antilles.

The components of beach/strand/dune vegetation are also widespread along the beaches of the world, and include *Baccharis halimifolia*, *Batis maritima*, *Borrichia arborescens*, *Canavalia maritima*, *Coccoloba uvifera*, *Ipomoea pes-caprae*, *Portulaca quadrifida*, *Spartina juncea*, *Sporobolus virginicus*, *Suriana maritima*, *Tournefortia gnaphalodes*, and *Turnera diffusa*. Rocky coasts and rock pavement support *Agave legrelliana*, *Borrichia arborescens*, *Conocarpus erectus*, *Erithalis fruticosa*, *Flaveria linearis*, *Heliotropium humifusum*, *Lithophila muscoides*, *Opuntia dillenii*, *Rachicallis americana*, *Sesuvium portulacastrum*, *Strumpfia maritima*, and *Trianthema portulacastrum*.

Many members of the freshwater herbaceous bog/marsh/swamp formation (Fig. 3.62) are also found throughout the Caribbean region, and at the generic level they are nearly cosmopolitan. There are grasses, sedges (*Cyperus giganteus*, *Eleocharis cellulosa*, *Scirpus*), cattails (*Typha domingensis*), *Caladium arborescens*, *Thalia geniculata*, and trees and shrubs from the wet phases of the lower to upper broad-leaved montane forest, including *Acoelorraphe wrightii*, *Annona glabra*, *Bucida buceras*, *Chrysobalanus icaco*, *Fraxinus caroliniana*, *Hibiscus elatus*, *Salix longipes*, and *Tabebuia angustata*.

Among the floating or rooted aquatics of Cuba are *Brasenia schreberi*, *Cabomba piauhyensis*, *Limnocharis flava*, *Myriophyllum sparsiflorum*, *Najas*, *Nelumbo lutea*, *Nuphar advena*, *Nymphaea ampla*, *N. odorata*, *Nymphoides grayana*, *Polygonum portoricense*, *Potamogeton illinoensis*, *P. nodosus*, and *Vallisneria neotropicalis*.

Genera characteristic of the beach/strand/dune, bog/marsh/swamp, or aquatic formations are not known as fossils from the Greater Antilles, although *Cabomba*, *Hibiscus*, *Thalia*, and *Typha* are known from Mexico and Central America, and some microfossils of the Cyperaceae and Poaceae may include members of these plant formations. They were undoubtedly present, but not preserved or yet recovered.

Figure 3.66. Open pine woodland on serpentine, Nipe Mountains (Loma Mensura in background), Cuba. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

The lower to upper montane broad-leaved forest grows inland from the mangrove, beach/strand/dune, freshwater herbaceous marsh/swamp, and aquatic formations in the lowlands of Cuba, particularly on the wetter northern coast. The habitats were formerly occupied by a paratropical rain forest, as evident from isolated remnants of this community left in the intensely cultivated farmlands. MAP is 1200–1600 mm, but there is a three-to-five-month dry season, probably recently enhanced by extensive cutting of the forest (see Hispaniola below). The tallest trees were probably *Ceiba pentandra* (30–40 m) associated with *Bucida buceras*, *Chlorophora tinctoria*, *Cordia collococca*, *C. gerascanthus*, *Ficus* sp., *Guazuma ulmifolia*, *Lonchocarpus domingensis*, *L. latifolius*, *Luehea speciosa*, *Mastichodendron foetidissimum*, *Peltophorum adnatum*, *Pithecellobium cubense*, *Roystonea regia*, and *Samanea saman*.

A phase of the lower to upper montane broad-leaved forest is the alluvial or riverside gallery forest, and it includes *Acoelorraphe wrightii*, *Bucida buceras*, *Calophyllum antillanum*, *Calyptronoma dulcis*, *Conocarpus erectus*, *Crescentia cujete*, *Dalbergia ecastaphyllum*, *Ficus subscabrida*, *Ginoria americana*, *Guettarda combsii*, *Hibiscus elatus*, *Lonchocarpus domingensis*, *Lysiloma bahamensis*, *Myrsine cubana*, *Roystonea regia*, *Sabal japa*, *Swietenia mahagoni*, *Tabebuia angustata*, and *Tabernaemontana amblyocarpa*.

As the moisture-laden trade winds from off the Atlantic Ocean begin to rise along the northern and eastern mountain slopes (e.g., Sierra Rosario, Sierra Maestra; Fig. 3.63; Appendix 1.5), annual rainfall increases from 1100–2400 mm to a maximum 3200 mm at ~800 m, providing more typical habitats for the lower to upper montane broad-leaved forest (montane rain forest and wet montane forest in the terminology of Holdridge [1947a, 1967; Holdridge et al., 1971]). The trees reach 30–35 m in height, the leaves are mostly mesophylls, and the nearly closed upper canopy is composed of the buttressed *Carapa guianensis* with the strangler vine *Clusia rosea*. The second canopy is 20–25 m in height, the leaves are mostly notophylls

Figure 3.67. Lowland pine forest, Moa Range, between Moa and Punta Gorda, Holguín, Cuba. From Borhidi (1996). Used with permission of Akadémiai Kiadó, Budapest.

and microphylls, and the canopy is more open. In the Sierra Maestra at altitudes between 1600 and 1900 m, with MATs of 10°–14° C and MAPs of 2800–3200 mm, there is a cloud or mossy forest association (Fig. 3.64). Characteristic species are

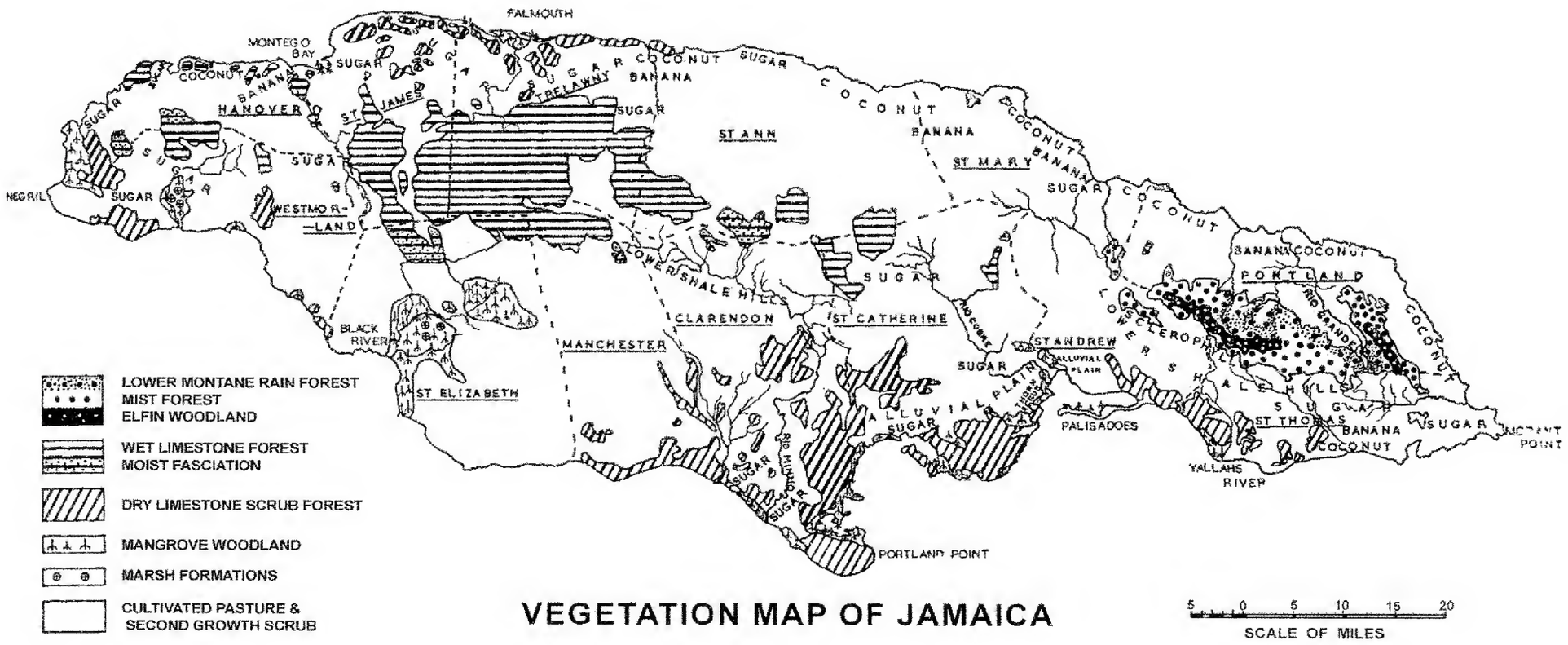


Figure 3.68. Vegetation map of Jamaica. From Asprey and Robins (1953). Used with permission of the Ecological Society of America.

the ferns *Alsophila aspera*, *Cyathea arborea*, and *Lophosoria quadripinnata*, with *Cyrilla racemiflora*, *Eupatorium paucibracteatum*, *Garrya fadyenii*, *Myrsine microphylla*, *Nectandra reticularis*, *Persea anomala*, *Sapium maestrense*, *Symplocos leonis*, *Torralbasia cuneifolia*, *Weinmannia pinnata*, and fern lianas *Dennstaedtia*, *Gleichenia*, and *Odontosoria* forming a dense tangle on the forest floor. At the highest elevations (e.g., Pico Turquino), above the zone of moisture condensation, the winds are strong, runoff is rapid, and the vegetation is a stunted, gnarled elfin forest or woodland (Figs. 3.64, 3.65). Members of the Ericaceae, Caprifoliaceae (e.g., *Viburnum villosum*), and various succulents (*Agave pendentata*) are common, along with *Eupatorium paucibracteatum*, *Ilex cubana*, *Lobelia cacuminis*, *Lyonia calycosa*, *Myrica cacuminis*, *Peratanthe cubensis*, *Persea similis*, *Torralbasia cuneifolia*, *Vernonia parvuliceps*, *V. praestans*, and *Weinmannia pinnata*.

In the Cenozoic fossil record of the Antilles, members of the lower to upper montane broad-leaved forest, particularly those in the slightly inland and upland subcanopies, are well represented. Among the genera from this zone reported as microfossils are *Lycopodium*, *Cyathea*, *Hemitelia* (*Cnemidaria*), *Lygodium*, *Podocarpus*, *Alchornea*, *Brunellia*, *Bursera*, *Casearia*, *Celtis*, *Chrysophyllum*, *Dendropanax*, Ericaceae, *Eugenia* type, *Faramea*, *Guarea*, *Ilex*, *Marcgravia*, *Myrcia*, *Rauwolfia*, *Smilax*, and *Zanthoxylum*.

Coniferous forest, pine, and pine-oak associations of *Pinus* (Figs. 3.66, 3.67) occur on nutrient-poor latosols primarily on the western and eastern ends of the island, and on the Isla de la Juventud, where pine forest is locally the dominant vegetation. The principal trees are *Pinus caribaea*, *P. cubensis*, *P. elliottii*, and *P. tropicalis*, often with an understory of grasses (e.g., *Panicum longiligulatum*) associated with palms (*Colpothrinax wrightii*) and other plants (*Byrsonima crassifolia*, *Curatella americana*) to form a kind of disturbed savanna. Oaks (*Quercus minima*, *Q. oleoides*, *Q. pumila*, *Q. sagraeana*, *Q. virginiana*) grow mixed with pines in western Cuba, and in pre-settlement times probably formed pine-oak forests comparable to the more extensive versions found in Mexico and northern Central America. The present edaphic control of *Pinus* is strong, and in the absence of sufficient paleobotanical information, it is difficult to know how its distribution was affected by moderate changes in climate at the middle to lower latitudes.

Jamaica

The vegetation of Jamaica is known from the summaries on ferns by Proctor (1985) and on flowering plants by Adams (1972) and Asprey and Robbins (1953). It is clear from the logs of the early Spanish explorers that all the Caribbean islands, including Jamaica, formerly had extensive forests:

> "The sky, air, and climate were just the same as in other places; every afternoon there was a rain squall that lasted for about an hour. The admiral writes that he attributes this to the great forests of that land." (From the biography of Christopher Columbus, Colón, 1959; see also early descriptions of the vegetation of other Caribbean islands by Abbad y Lasierra, 1866; Eggers, 1879; Hill, 1899; Melgarejo, 1914; Murphy, 1916)

A vegetation map is shown in Fig. 3.68, and representative plants of Jamaica are arranged according to the plant formations recognized here in Appendix 1.6. Some names

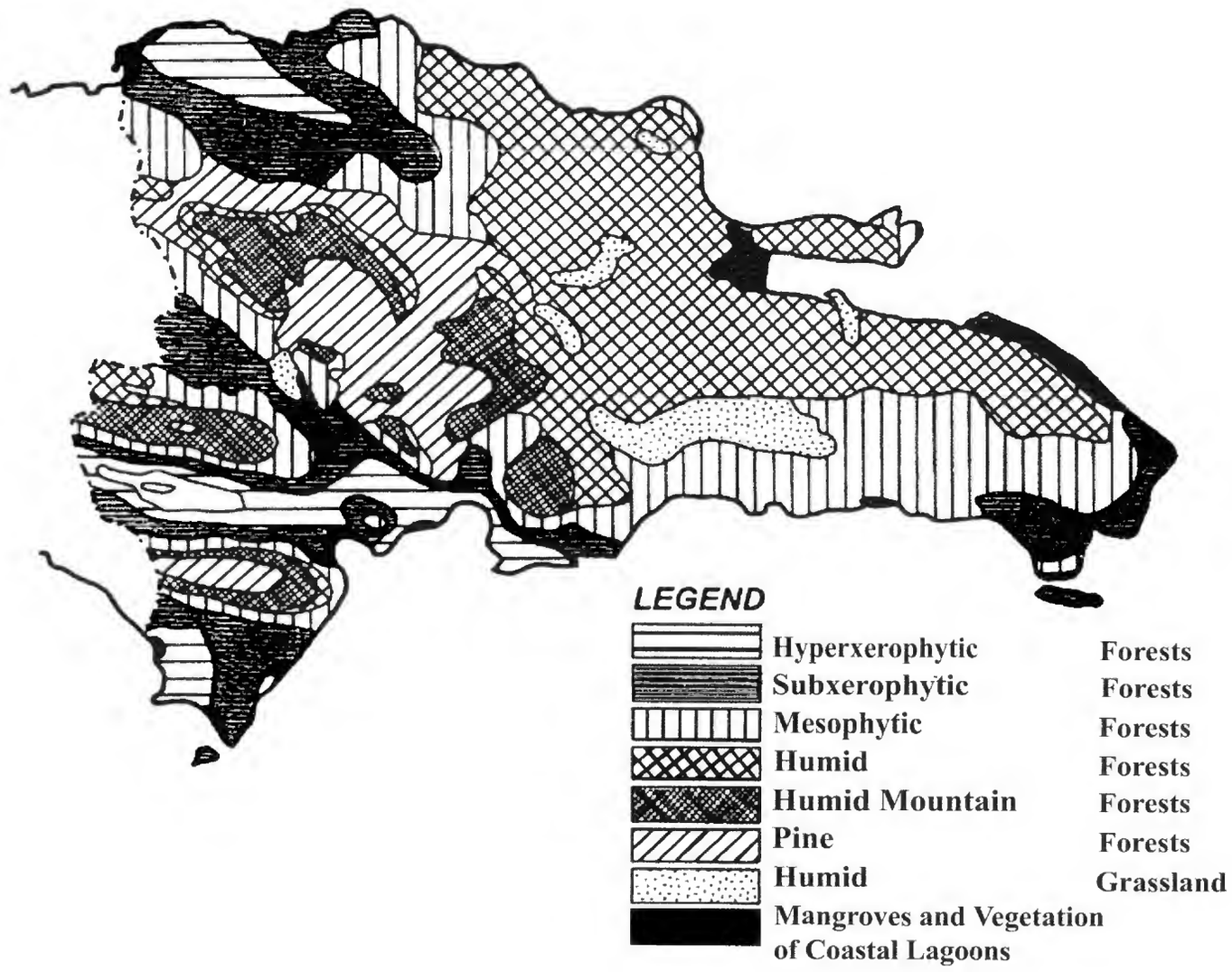


Figure 3.69. Vegetation map of the Dominican Republic. From Bolay (1997). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

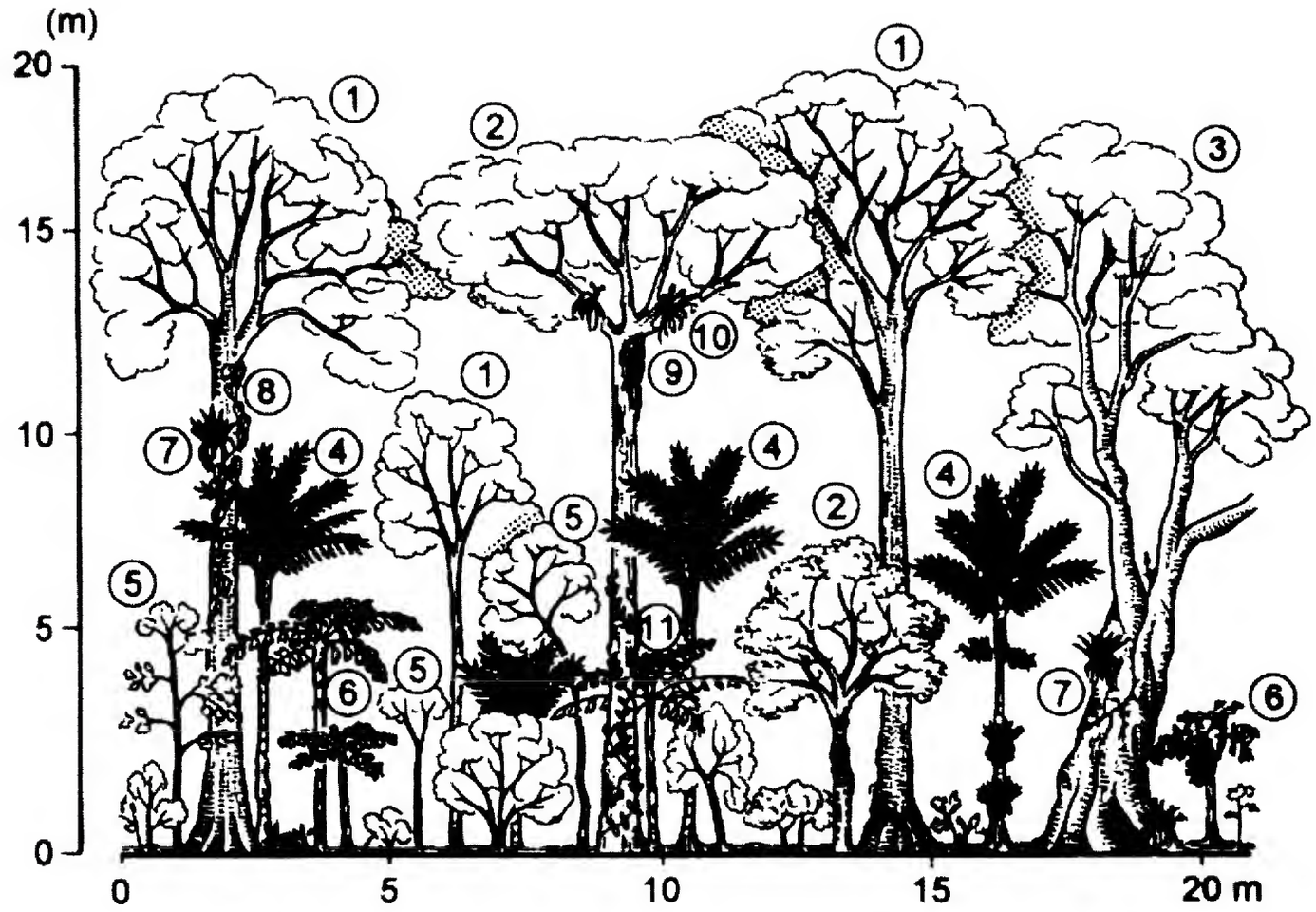


Figure 3.70. Profile of primary rain forest (wet phase of lower to upper montane broad-leaved forest) near Loma Quinta Espuela (above 700 m), Dominican Republic. 1 = *Mora abbotti*; 2 = *Cyrilla racemiflora*; 3 = *Didymopanax tremulus*; 4 = *Prestoea montana*; 5 = Myrtaceae; 6 = *Cyathea arborea*; 7 = *Vriesea capituligera*; 8 = *Philodendron* sp.; 9 = *Rhipsalis baccifera*; 10 = Orchidaceae; 11 = *Marcgravia rectiflora*. From Bolay (1997). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

are familiar because the plants are widespread and are part of the vegetation of Mexico and Cuba discussed earlier—*Batis maritima*, *Uniola virgata*, *Rhizophora mangle*, etc. Others are more characteristic of Jamaica or are part of the extensive endemic flora of the island (27.9% of the vascular plants). At the generic level, these endemics include *Dendrocousinsia*, *Jacaima*, *Peltostigma*, and *Tetrasiphon* (Howard, 1973). A single fossil flora is known from microfossils in the middle Eocene Guys Hill (Chapelton) Formation.

Hispaniola

The vegetation and plant communities of Hispaniola (countries of Haiti and Dominican Republic) are in many respects similar to those of adjacent Cuba, but they are distributed over a smaller land area (76,484 km^2 compared to 110,861 km^2), and Haiti in particular has been subjected to extreme environmental devastation. Estimates of the remaining natural plant cover of Haiti range as low as 1% with corresponding reduced capacity to withstand natural disasters:

> "The floods of 24 May 2004 and the tragic loss of thousands of lives in southeastern Haiti and Jimaní, Dominican Republic, provide important lessons for scientists, conservationists, and politicians. The same storm did not have such a devastating effect in neighboring Puerto Rico or in other regions of Dominican Republic, mainly because the highlands are forested." (Aide & Garu, 2004)

With reference to the Dominican Republic (from an interview with Rosa Encarnación, age 85, Dominican Republic, 1983; Bolay, 1997):

> "Look here, in the past these mountains were densely covered with forests, and it rained a lot. You must know, May ended as it had begun, rain, rain, rain…! During May it rained all the time. Not just once a day, seven and eight times a day torrential rains came down from the sky. In the past moss covered the walls of huts and sometimes good water came from the roofs. There was plenty of water. It rained day and night. It is different today. There is a lot missing here, due to the lack of water. I do not know what is wrong today."

Some faint hope for better times exists through the efforts of small cadres of scientists working under formidable political indifference. There are outside projects such as the restoration and databasing of the E. L. Ekman Herbarium at the National Herbarium of Haiti by Martin Dube and J. A. Constant through the Agence Universitaire de la Francophonie, a consortium of French-speaking nations supporting research. Although duplicate collections are in Sweden and at the Institute of Jamaica, Kingston, these activities on site in Haiti are preserving some local interest in natural history that hopefully will persist until more rational and ethical political policies return. There is a recent land cover map of Haiti (UNOPS, 2001), and Judd (1987) has published on the vegetation of two national parks in the country (see below).

Hispaniola has a considerable range in elevation from sea level to the highest point in the Antilles (Pico Duarte). Equally important is that with compression of the island against the Bahamas Platform beginning in the middle Eocene and subsequent shearing throughout the Cenozoic by the eastward movement of the Caribbean Plate, a series of uplands and valleys

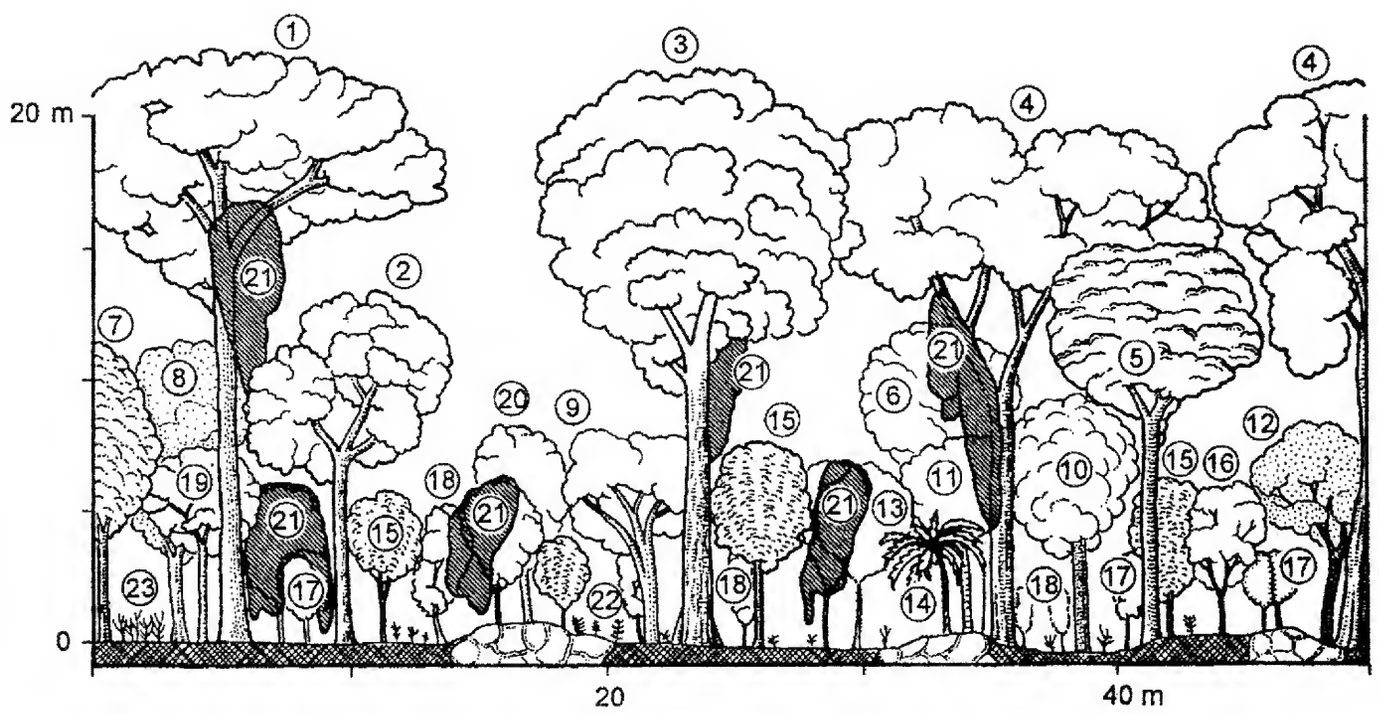


Figure 3.71. Profile of deciduous forest on limestone, near Manuel Goya, Dominican Republic. 1 = *Spondias mombin*; 2 = *Acacia scleroxyla*; 3 = *Guazuma ulmifolia*; 4 = *Bursera simaruba*; 5 = *Guaiacum sanctum*; 6 = *Mastichodendron foetidissimum*; 7 = *Coccoloba diversifolia*; 8 = *Antirhea lucida*; 9 = *Cassia emarginata*; 10 = *Ficus velutina*; 11 = *Clusia rosea*; 12 = *Chrysophyllum olviforme*; 13 = *Trichilia hirta*; 14 = *Crescentia cujete*; 15 = *Eugenia foetida*; 16 = *Salvia sessilifolia*; 17 = *Myrciaria floribunda*; 18 = *Amyris* sp.; 19 = *Capparis indica*; 20 = *Thouinia trifoliata*; 21 = *Gouania lupuloides*; 22 = *Kalanchoe pinnata*; 23 = *Ocimum* sp. From Bolay (1997). Used with permission of Margraf Publishers, GmbH, Weikersheim, Germany.

have been created (Fig. 1.16) that provide habitats for a variety of vegetation types (Fig. 3.69). The Dominican Republic has a comparatively good record of designating natural areas and some success in preserving them. The Dirección Nacional de Parques (DPN) maintains national parks and scientific nature preserves that presently include ~11.2% of the country (Bolay, 1997, pp. 69–77). These, like those in Mexico, Costa Rica, and Panama, are important for studies of vegetation history in northern Latin America because they preserve analogs of the paleocommunities, they are a source of material for spore and pollen reference collections and leaf margin analysis, and they could be the sites of modern pollen rain studies.

A bibliography of papers on the vegetation of Hispaniola is provided by Zanoni et al. (1984); vegetation maps for the Dominican Republic are given by Ciferri (1936), Moscoso (1943), and Tasaico (1967); profiles through the montane broad-leaved forest of the Dominican Republic are shown in Figs. 3.70 and 3.71; and the pine forests of Haiti are described by Holdridge (1942, 1947b). The remaining vegetation of Haiti is best preserved in two national parks in the southwestern peninsula of the island and surveyed by Judd (1987). In the Parc National Pic Macaya, in the Massif de La Hotte at the far southwestern end of the island, the vegetation is a wet forest on limestone between 800 and 1250 m, with a complex of pine forest (*Pinus occidentalis*; Holdridge, 1942, 1947b) and cloud forest at the higher elevations. At Parc National La Visite, in the Massif de la Selle to the east, pine forest grows in a bowl-shaped depression in a plateau with cloud forest on the north-facing slopes and in ravines. Endemism among the vascular plants on the mountain peaks is 29% and 34%, respectively. The characteristic plants of these communities listed by Judd (1987) are given in Appendix 1.7

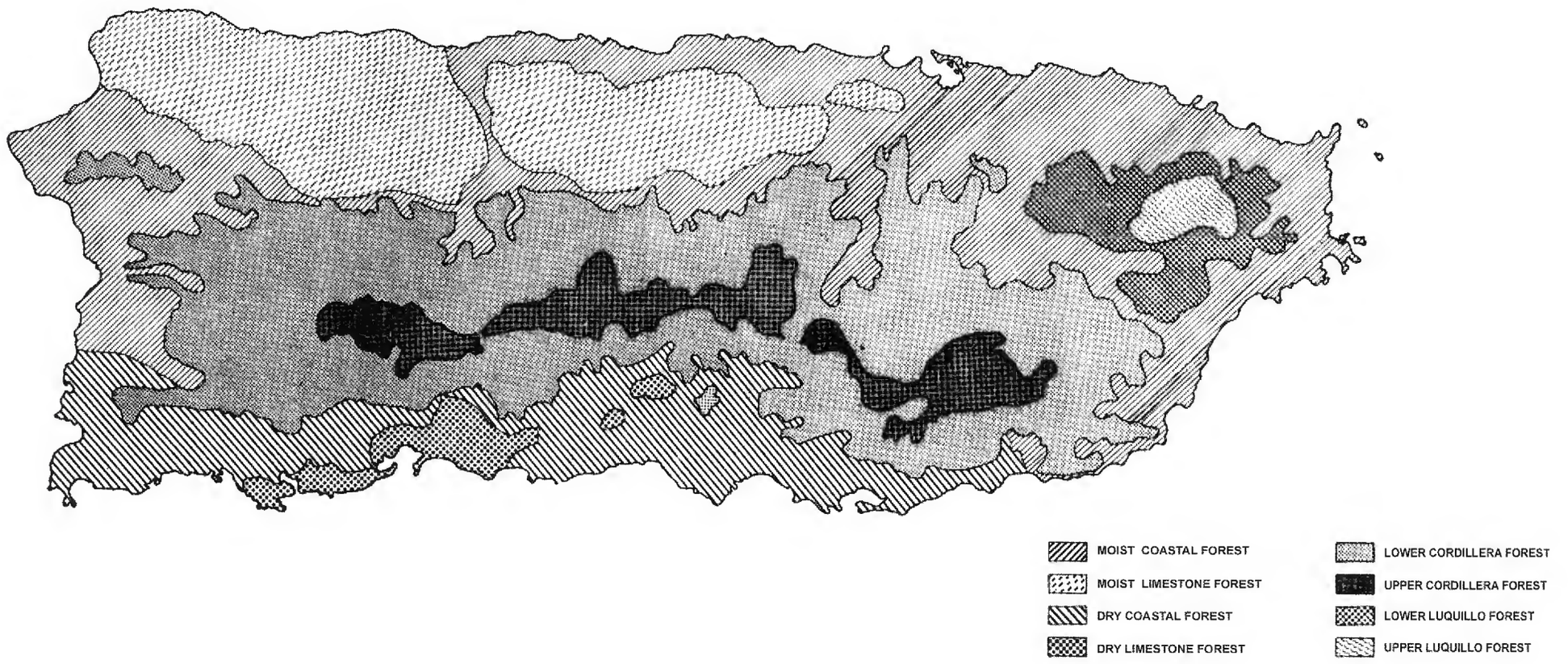


Figure 3.72. Vegetation map of Puerto Rico. From Little and Wadsworth (1964; see also Helmer et al., 2002), courtesy of U.S.D.A. Forest Service.

Puerto Rico

The vegetation of Puerto Rico is known through the studies of Britton and Wilson (1923 et seq.), Gleason and Cook (1926), Little and Wadsworth (1964), Little et al. (1974), Odum (1970), Ewel and Whitmore (1973), Liogier (1985, 1988), Liogier and Martorell (1982), Proctor (1989), Figueroa Colón (1996), and others.

The island has ~364,000 ha of closed forest covering ~41.5% of the land. Little and Wadsworth (1964) estimate there are ~500 species of trees on Puerto Rico, and they arrange these into eight forest types (Fig. 3.72). There is a new forest map based on Landsat imagery (Helmer et al., 2002) using the classification of Areces-Mallea et al. (1999). The map does not include representative species, so the one of Little and Wadsworth (1964) is given in Fig. 3.72, and their system and the one used here are given in Appendix 1.8. Helmer et al. (2002) provide a comparison of the various classification systems used for Puerto Rican vegetation.

Dry areas with serpentine soils support cacti (*Cactus intortus*), *Agave*, *Plumeria*, and other plants of a near-desert community (Fig. 3.73). The coast in many areas is fringed by mangroves, and inland or in less saline waters there are freshwater swamps often dominated by *Pterocarpus officinalis* (Fig. 3.74) or by remnants of a lowland Neotropical rain forest. In the lower to upper broad-leaved montane forest formation the wettest associations are transitional to the former near-lowland Neotropical rain forest (e.g., Figs. 3.75, 3.76 from Dominica), the driest associations are transitional to the shrubland/chaparral–woodland–savanna formation, and the formation includes several phases resulting from local habitat conditions (e.g., concentrations of ferns, palms; the seral *Cecropia*). One of the largest expanses of the broad-leaved montane forest in the Antilles is at El Verde in the Luquillo Mountains of Puerto Rico (Figs. 3.77–3.83). It was set aside by the Division

Figure 3.73. Shrubland/chaparral–woodland–savanna (near desert) on serpentine west of Yauco, Puerto Rico. *Cactus intortus*, *Agave missionum* in foreground; *Plumeria alba* in center; *Andrachne cuneifolia* tall leafless shrub in back. From Gleason and Cook (1926). Used with permission of Blackwell Publishing, Oxford, U.K.

Figure 3.74. *Pterocarpus officinalis* with mangrove fern *Acrostichum aureum*, and liana *Paullinia pinnata*, Humacao Playa, Puerto Rico. From Gleason and Cook (1926). Used with permission of Blackwell Publishing, Oxford, U.K.

Figure 3.75. Montane forest of Dominica with three largest trees in foreground, *Euterpe dominicana* (left), *Symphonia globulifera* (center), and *Tovomita* (right). From Beard (1949). Used with permission of Oxford Forestry Institute.

of Biology and Medicine (DBM) of the U.S. Atomic Energy Commission (USAEC) to test the effects of radiation on forests, and an inventory of the vegetation was prepared by the U.S. Forest Service.

The sequence of plant communities from low to high elevations is the agricultural lowlands, tabonuco forest (*Dacryodes excelsa*), Colorado forest (*Cyrilla racemiflora*), palmbreak (sierra palm, *Euterpe globosa*), and elfin forest (Howard, 1968). Among the eight forest types recognized by Little and Wadsworth (1964), the tabonuco is included in their Lower Luquillo forest, and the Colorado, palmbreak, and elfin in their Upper Luquillo forest. The composition of each of these communities is presented in Appendix 1.8. The number of species is estimated at 830 and includes ~250 kinds of trees (Figueroa Colón, 1996). As one of the easternmost islands of the Greater Antilles, Puerto Rico frequently receives the full force of hurricanes. During two days of September 1928, 635 mm (25 in) of rain fell in the Luquillo Mountains and there was severe damage from winds and landslides. Openings in the forest are populated by *Cecropia peltata*, a common successional plant widespread in the American tropics (see Chapter 1, Mexico; Fig. 1.12). The genera of plants for the Greater Antilles mentioned in the text are listed and arranged into plant formations in Appendix 1.9.

Figure 3.76. *Symphonia globulifera*, Dominica. From Beard (1949). Used with permission of Oxford Forestry Institute.

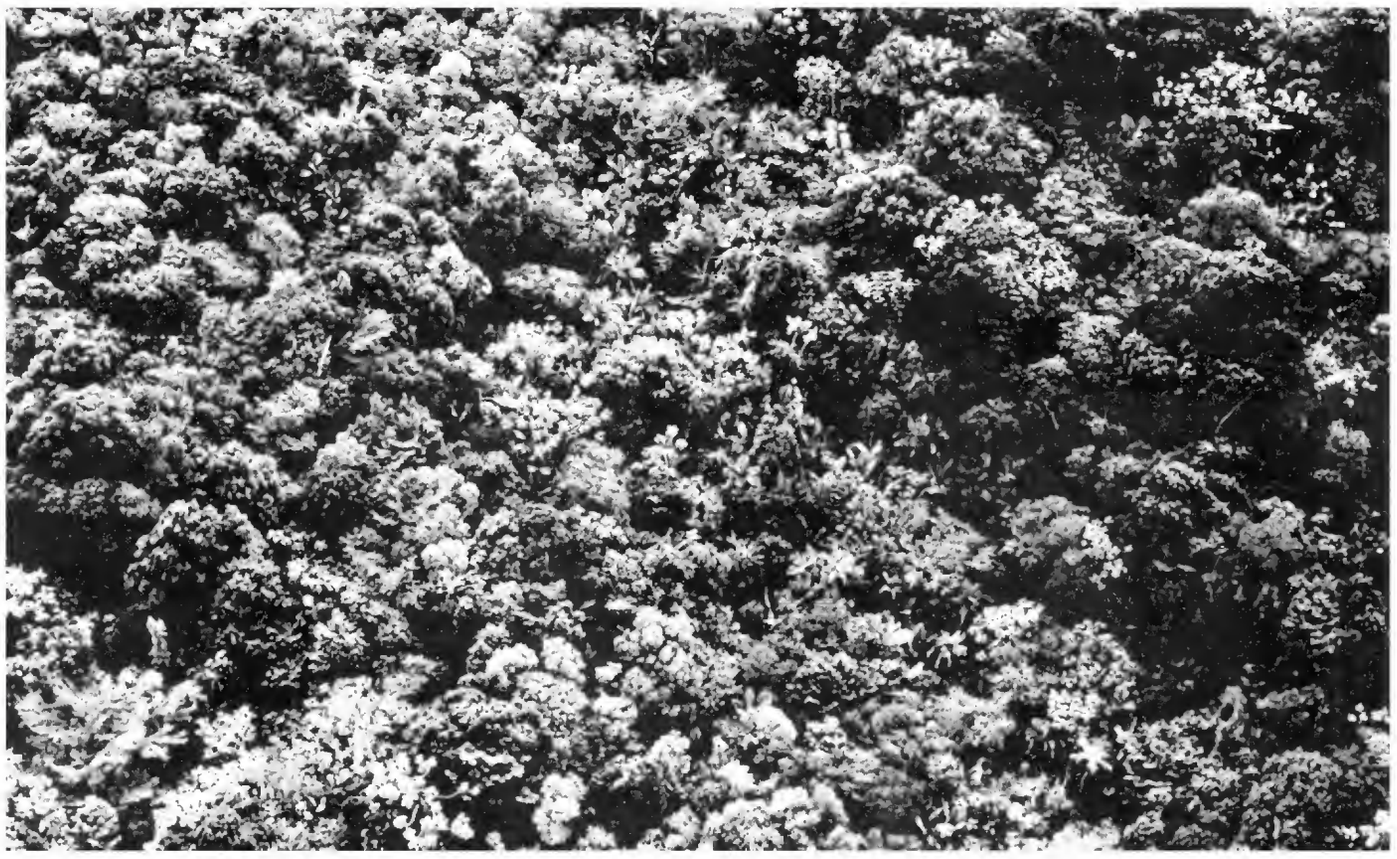


Figure 3.77. Luquillo experimental forest (lower to upper montane broad-leaved forest), Puerto Rico. From Odum (1970). Courtesy of U.S. Atomic Energy Commission.

Figure 3.78. Interior of Luquillo experimental forest (montane broad-leaved forest), Puerto Rico. Photograph from U.S. Forest Service Historical Photograph Collection.

Figure 3.79. *Cnemidaria horrida* and *Cyathea arborea* (taller, center) in the Luquillo Mountains of Puerto Rico. From Tryon and Tryon (1982). Used with permission of Springer Verlag, Berlin.

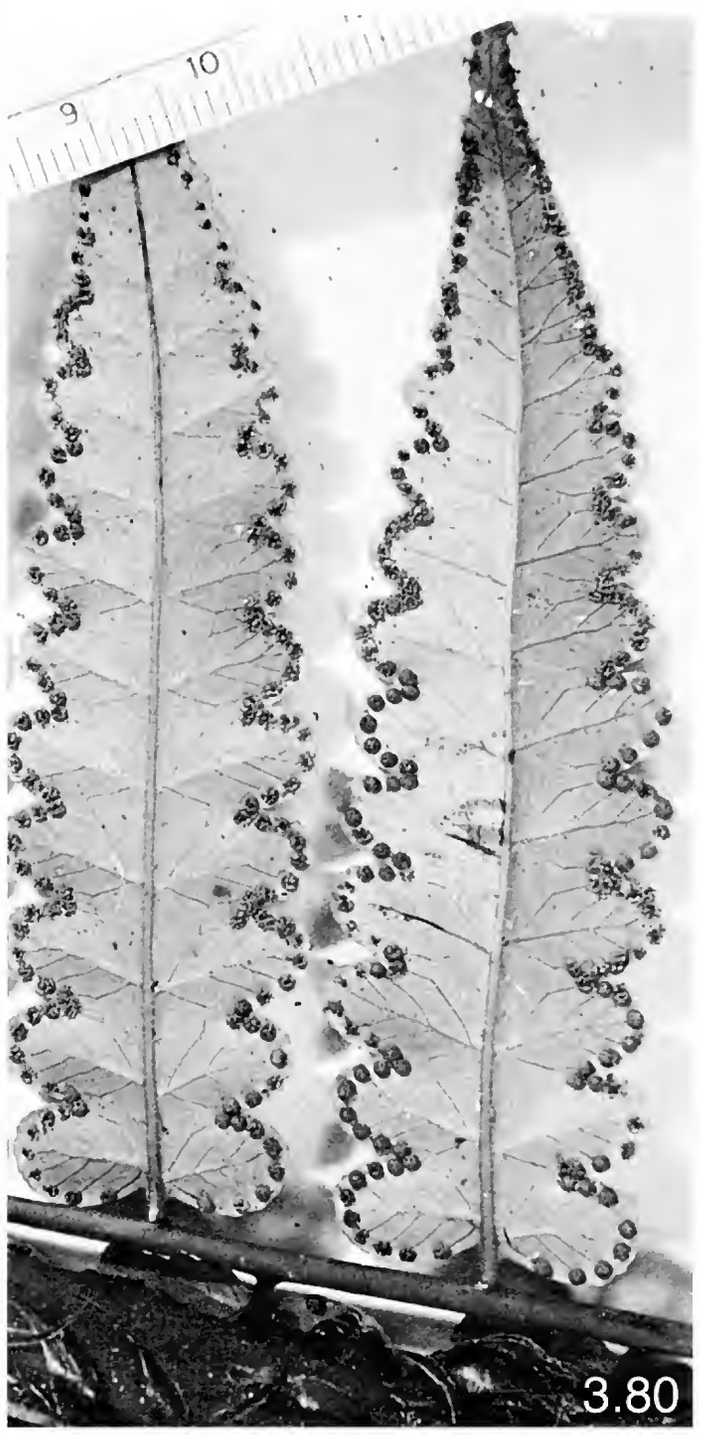
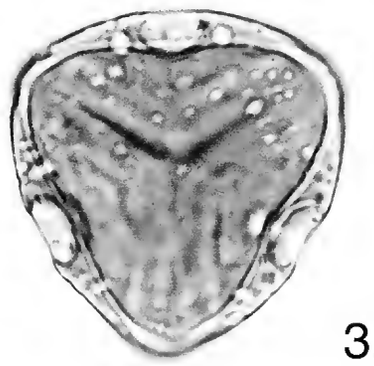
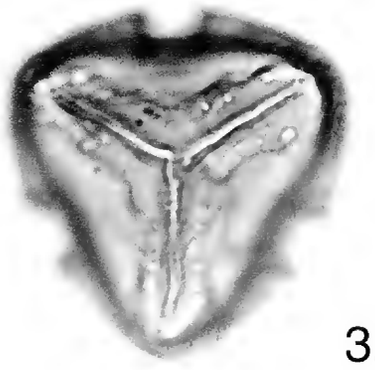


Figure 3.80. Sori (clusters of sporangia) on leaf of *Cnemidaria petiolata*, Barro Colorado Island, Panama. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.





Figures 3.81, 3.82. Modern spore of *Cnemidaria horrida*. 3.81—Polar view, margin. 3.82—Polar view, surface.

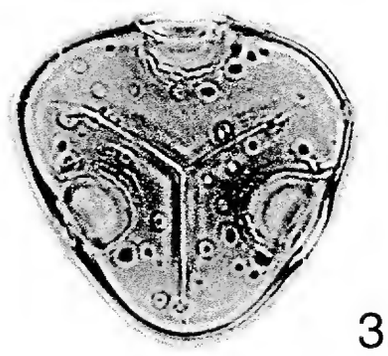


Figure 3.83. Fossil spore of *Cnemidaria* from the Miocene Gatún Formation, former Canal Zone, Panama.

CENTRAL AMERICA

The geologic structures, edaphic characteristics, topography, and climates of northern Central America (Guatemala, Belize, Honduras, El Salvador, northern Nicaragua) are a continuation of those described for southern Mexico, but there are differences. One is that the topography is more subdued. Also, the land continues to narrow in a funnel-shaped configuration toward the south—it is only 48 km across the Isthmus of Panama at its narrowest point. There are several consequences of these physical features, and one is that there is no extensive grassy páramo in Central America. The highest altitude vegetation is shrubby subpáramo in the terminology used for the northern Andes (see Chapter 3, Colombia). Another is that many plants are common to Mexico, Guatemala, and northern Nicaragua, a region recognized by Rzedowski (1991) as "Megamexico" (southern United States–northern Mexico to the Nicaragua Depression at Lago Nicaragua; see also Islebe & Velázquez, 1994). Within Megamexico and between this region and southern Central America, there are other trends and differences. For example, the number of temperate elements with northern affinities diminishes southward as high-altitude habitats become restricted. In contrast, tropical elements with South American affinities are abundant in the north where lowland habitats are available. As noted previously, even as far north as the coastal lowlands of southern Mexico, ~75% of the canopy trees have South American origins (Wendt, 1993).

The narrowing of the land southward also reduces continentality—the presence of drier habitats and greater climatic extremes in continental interiors removed from sources of moisture and the mollifying effects of large bodies of water (I: pp. 93–94, 189, 204). Although slope, exposure, and edaphi-

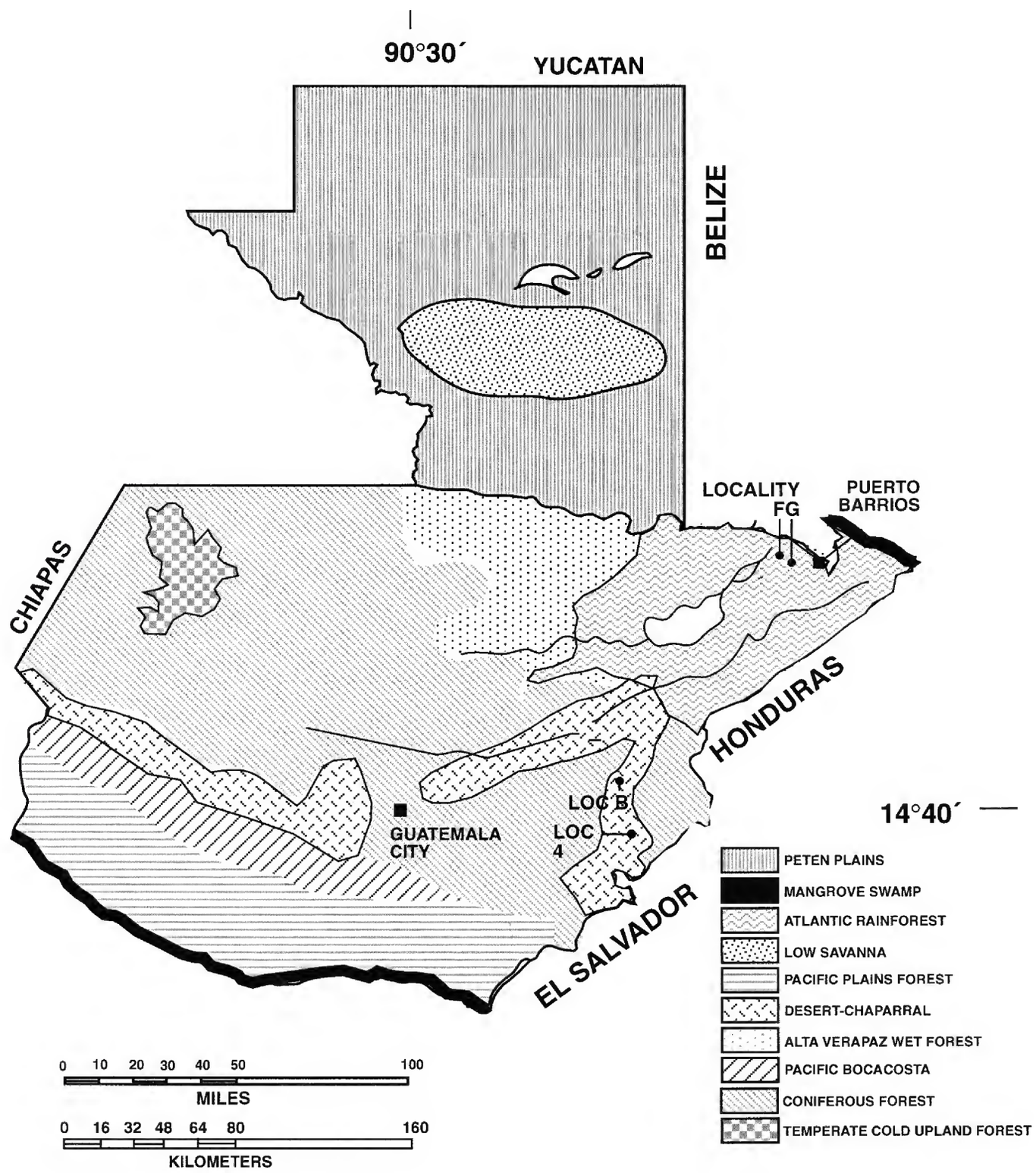


Figure 3.84. Vegetation map of Guatemala. After Standley and Steyermark (1945) and various sources. "Locality" designates plant microfossil sites (see Chapter 6).

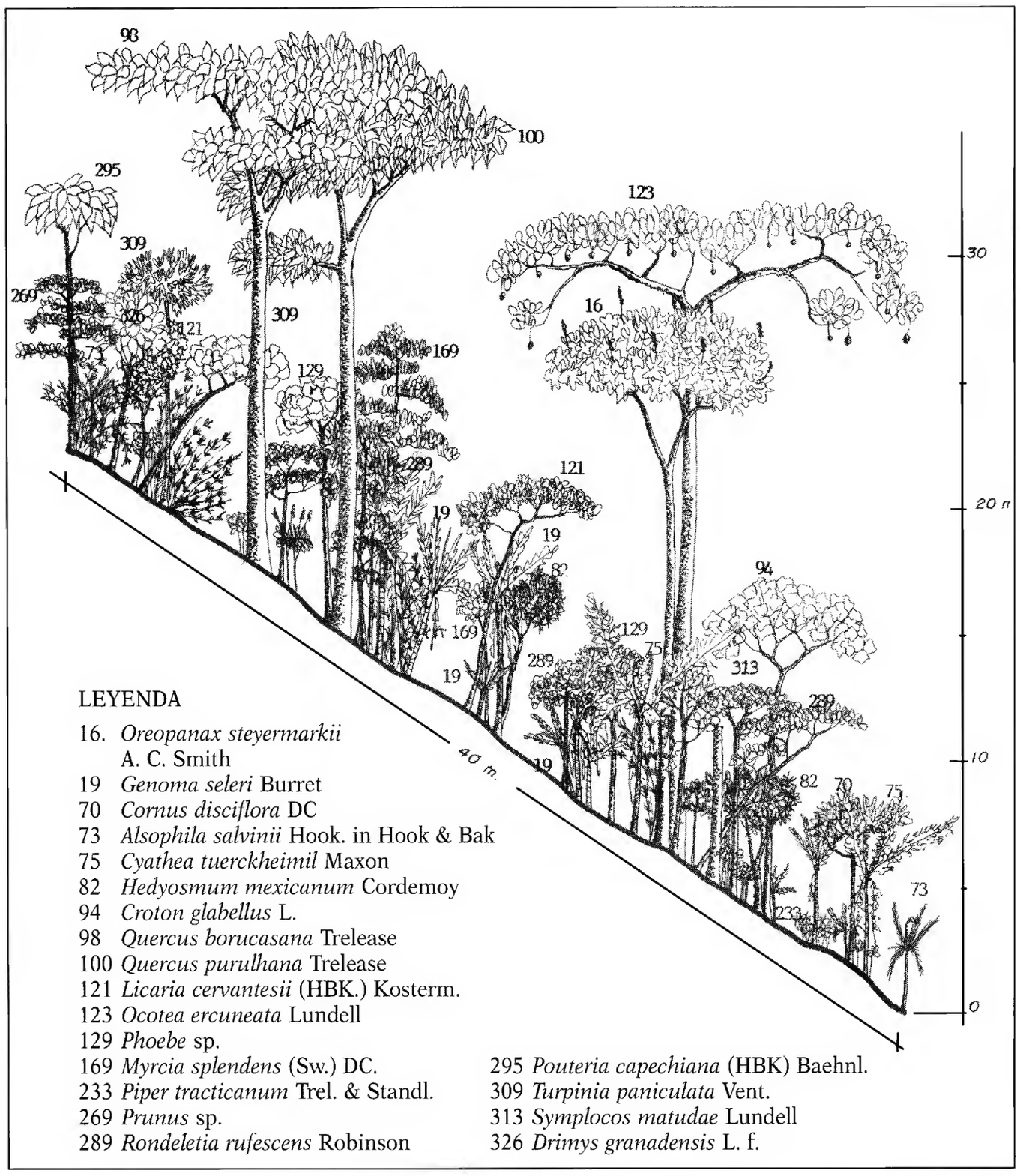


Figure 3.85. Cloud forest at 2000 m, Biotopo de Quetzal "Lic. Mario Dary Rivera," Parulhá, Baja Verapaz, Guatemala. From Islebe and Vélez Pérez (2001). Used with permission of Editorial INBio, Santo Domingo de Heredia, Costa Rica.

cally controlled dry areas occur in Central America, without augmentation by continentality even the most arid regions receive more moisture than the interior of Mexico. Also, there are no cold currents offshore from Central America to produce desiccating coastal winds (the Humboldt Current bends westward near central Ecuador). As a result, the natural vegetation in the driest parts of Central America is dry deciduous forest (shrubland/chaparral–woodland–savanna) rather than desert. There are no extensive natural grasslands for the same reasons (too much rain, high humidity, low continentality), and because of edaphic and other factors.

The Central American region has been a connecting link between tropical biotas to the south and temperate ones to the north to varying degrees throughout the Late Cretaceous period and the Cenozoic era. During this time, climates also fluctuated between the hothouse interval of the Paleogene and the icehouse interval of the Neogene, and waves of plant and animal immigrants moved in both directions across the landscape in response to these changes. Biotic representatives from each region persisted and diversified, and presently they constitute a vascular flora conservatively estimated at about 15,000 species. This number is based on a flora of about 20,000 vascular plant species for Mexico, greater than 10,000 species for the Greater Antilles, and the following approximations for countries in Central America: Guatemala, 10,000 species (Williams, in Rzedowski, 1978, p. 73); Nicaragua, 5796 species (Stevens et al., 2001, p. xxxv); Costa Rica, 10,979 species (Instituto Nacional de Biodiversidad [INBio] Web site, Biodiversity in Costa Rica, http://www.inbio.eas.ualberta.ca); and Panama, 9529 species (ferns and allies 940, gymnosperms 20, angiosperms 8569 databased to date; Mireya Correa, pers. comm., 2001). Summaries of cloud forest vegetation are given in Kappelle and Brown (2001), local surveys have been made of submontane forests in El Salvador (Berendshon, 1991), there is the *Flora de Nicaragua* (Stevens et al., 2001), and the ongoing *Flora Mesoamericana* (Davidse et al., 1994 et seq.) will provide an inventory of the plants for that region estimated at about 18,000 species.

Figure 3.86. Pine forest of *Pinus caribaea* north of Bluefields, Nicaragua. From Wagner (1964). Photograph by J. J. Parsons.

Guatemala

The alpine and subalpine vegetation of Guatemala is comparatively well known from the studies of Islebe and Kappelle (1994; Islebe, 1996), and the highland vegetation of the Sierra de los Cuchumatanes was surveyed as part of modern pollen rain studies (Islebe & Hooghiemstra, 1995). General summaries are provided by Lundell (1937; Petén), Standley & Steyermark (1945), and Steyermark (1950), and there is a study of savannas and wetlands of adjacent Belize (Bridgewater et al., 2002). A vegetation map for Guatemala, based on Standley and Steyermark (1945) and Steyermark (1950), is shown in Fig. 3.84, and the composition of the plant formations recognized here is given in Appendix 1.10.

In Petén, the vegetation is a semi-evergreen forest dominated by *Brosimum alicastrum* (ramón), and it contributes 40%–60% of the modern pollen rain (Vaughan et al., 1985; Leyden, 1987). There are savannas with *Curatella americana*, *Byrsonima crassifolia*, and *Quercus oleoides*; pinelands of *Pinus caribaea*; and mesic forests in the uplands (>200 m) of *Alfaroa mexicana*.

Zonation is best developed in the high altitudes of the Sierra de los Cuchumatanes and consists of *Abies guatemalensis* forests (into northern Honduras; 2800–3400 m) on steep moist slopes, and *Juniperus standleyi–Pinus hartwegii* (3100–3800 m) associated with shrubs of *Aphanactis standleyi* and *Holodiscus argenteus* (Rosaceae), *Mahonia volcania* (Berberidaceae), *Oxylobus glanduliferus* (Asteraceae), and *Pernettya prostrata* (Ericaceae). At lower elevations, the prominent plants are the ferns *Alsophila* and *Cyathea*, and *Cornus*, *Drimys*, *Myrica*, *Oreopanax*, and *Quercus* as shown in the profile of cloud forest vegetation in Fig. 3.85. The pollen signature of the high-altitude communities is known from pollen rain studies on moss polsters at 2800–4200 m, and consists primarily of *Abies* and Asteraceae from the fir forest; *Juniperus*, *Buddleja*, and Gramineae from the subalpine forest zone; and *Pinus* (up to 90%), *Juniperus*, *Alnus* (40%), and *Hedyosmum* (0.8%) in all samples (Islebe & Hooghiemstra, 1995; Chapter 6).

Nicaragua

The vegetation of Nicaragua is known through the recent flora by Stevens et al. (2001; Stevens, 2001). There is no true desert, natural grassland, or páramo (the highest elevations are occupied by elfin forest). A number of northern temperate trees reach their southernmost distribution in the highlands of the Cordillera Yolaina to the west of Bluefields (Fig. 3.86) including *Juniperus*, *Pinus*, *Carpinus*, *Liquidambar*, and *Ulmus*. A

Figure 3.87. La Selva Biological Station, Costa Rica. Photograph by Donald Stone.

Figure 3.88. Tropical dry forest at Santa Rosa National Park, Costa Rica. Photograph by Tom Croat.

Figure 3.89. *Ceratopteris pteridoides* with *Nymphaea*, Turrialba, Costa Rica. From Tryon and Tryon (1982). Used with permission of Springer Verlag, Berlin.

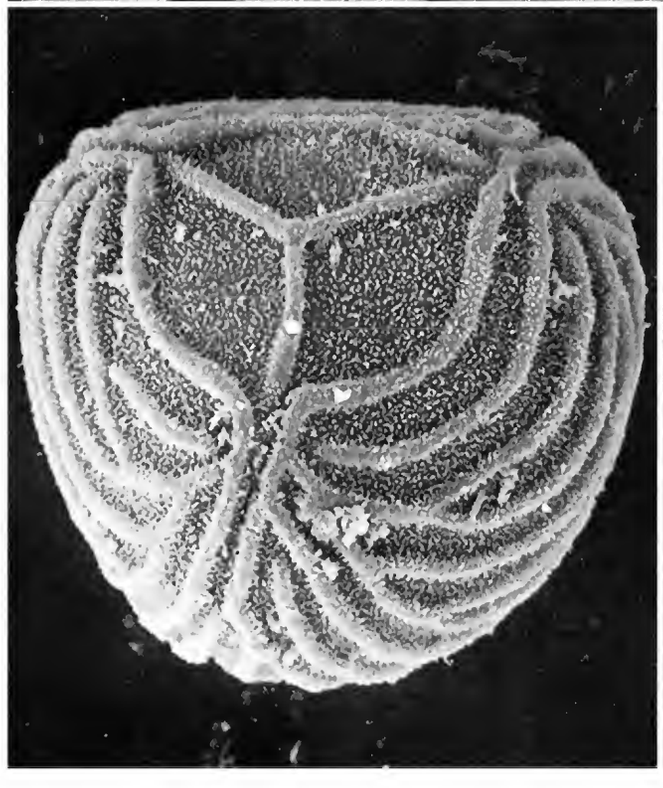


Figure 3.90 (left). Modern spore of *Ceratopteris cornuta*. From Tryon and Lugardon (1991). Used with permission of Springer Verlag, Berlin.

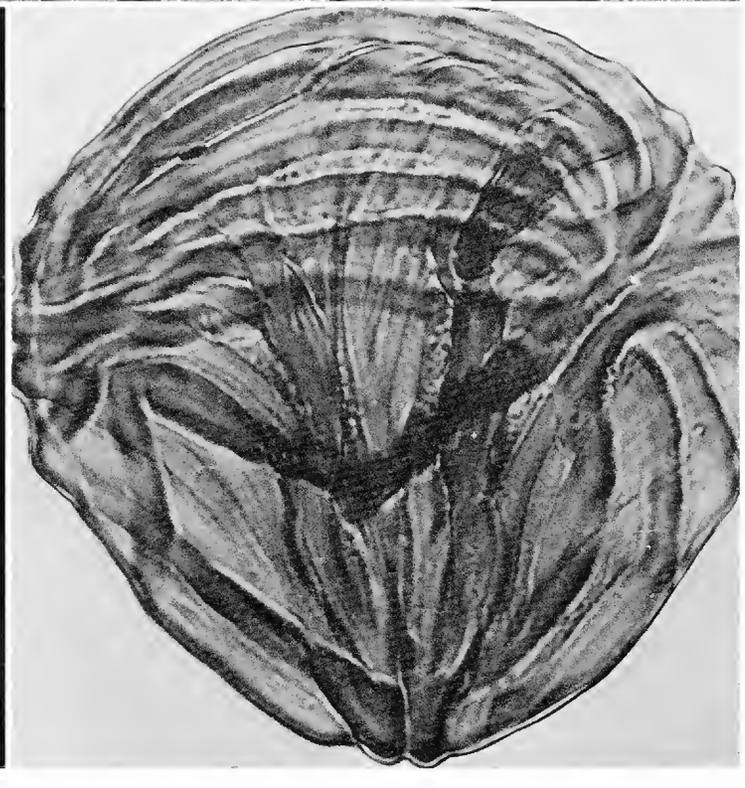


Figure 3.91 (right). Fossil spore of *Ceratopteris* from the Miocene Cucaracha Formation, former Canal Zone, Panama.

Figure 3.92. *Pelliciera rhizophorae*, Golfo Dulce, Costa Rica. From Allen (1956). Reprinted with permission of the University Press of Florida, Gainesville.

few extend farther south into southern Central America and South America such as *Alnus*, *Myrica* (not yet reported from Nicaragua but present to the north and south), *Juglans*, *Ostrya*, and *Quercus*. Others grew in northern Central America during the late Cenozoic but no longer occur there—*Abies*, *Picea*, *Acer*, *Fagus*, and *Platanus*. Six principal plant formations are recognized for Nicaragua, and in the summary in Appendix 1.11, the classification used by Stevens et al. (2001) is indicated in parentheses or in the subheadings.

Costa Rica

A tradition in Costa Rica important in interpreting biotic and environmental history is its impressive record of preserving natural habitats. The vegetation in these preserves serves as a valuable analog for reconstructing climate, physiography, lineages, and migrations through the region during the Cenozoic. Among these are the biological stations maintained or utilized by the Organization for Tropical Studies (OTS) at La Selva (Atlantic lowland rain forest, tropical wet forest zone, 29–400 m; McDade et al., 1994; Matlock & Hartshorn, 1999; Fig. 3.87), Refugio Rafael Lucas Rodríguez Caballero (formerly Palo Verde, Pacific deciduous dry forest, 3–183 m), Santa Rosa National Park (lowland deciduous forest, 0–320 m), Cerro de la Muerte (montane forest, 3000 m), Corcovado National Park (Pacific lowland rain forest, 0–400 m), and Las Cruces (premontane cloud forest, 1200 m). Monteverde (1200–1800 m; Nadkarni & Wheelwright, 2000) is a premontane wet forest–cloud forest–elfin forest community protected by early Quaker settlers and managed since 1971 by the Tropical Science Center (TSC). The numerous theses, dissertations, and other studies made possible by the preservation of these habitats have contributed significantly to our understanding of Neotropical communities (Janzen, 1983). Many of the results are published in *Biotropica*, the journal of the Association of Tropical Biology (ATB), and in *Brenesia*, the journal of the Museo Nacional de Costa Rica. In turn, this information lends paleoenvironmental meaning to fossil assemblages recovered from the region.

Extensive botanical explorations in Costa Rica were made by the Danish botanist Anders Oersted (1871; Grayum et al., 2004) and continue with the numerous studies currently facilitated by OTS and carried out by INBio, the Museo Nacional, and MO. During the intervening period, important contributions were made by Pittier (1908; "determined, indefatigable, tyrannical," Gómez & Savage, 1983), Standley (1937–1938), and Burger (1971, 1977). Additional lists and inventories are provided by Hartshorn (1983), Gentry (1990), Kappelle (1995, 1996), Wilbur (1994; La Selva), and Haber (2000; Haber et al., 1996; Monteverde), the *Manual de Plantas de Costa Rica* (Hammel

Table 3.6. Extent of the Holdridge life zones in Costa Rica (after Hartshorn, 1983, p. 123, based on Holdridge et al., 1971).

Life zone	Extent km^2	Percentage (%)
Tropical dry forest	5263	10.3
Tropical moist forest	12,366	24.2
Tropical wet forest	11,549	22.6
Tropical premontane moist forest	2402	4.7
Tropical premontane wet forest	6950	13.6
Tropical premontane rain forest	5008	9.8
Tropical lower montane moist forest	102	0.2
Tropical lower montane wet forest	767	1.5
Tropical lower montane rain forest	3781	7.4
Tropical montane wet forest	51	0.1
Tropical montane rain forest	2759	5.4
Tropical subalpine rain páramo	102	0.2

Figure 3.93. Lowland tropical rain forest preserved in the Organization for Tropical Studies La Selva Biological Station, Costa Rica. Photograph by Sally Horn.

et al., 2003 et seq.), and the *Páramos de Costa Rica* (Kappelle & Horn, 2005). A digital flora of the La Selva Biological Station based on living plants and herbarium specimens is under way at OTS (http://sura.ots.ac.cr/local/florula3/index.htm). The flora is estimated at ~9300 vascular plants. The 12 life zones recognized for Costa Rica by Holdridge (1967; Holdridge et al., 1971) are given in Table 3.6 and Appendix 1.12, arranged according to the system used here, together with representative members of each vegetation type.

There are no deserts in Costa Rica as traditionally defined. The driest communities belong to the shrubland/chaparral–woodland–savanna formation (tropical dry forest). They occur along the northwest coast of Costa Rica around the Golfo de Nicoya and northward from the Nicoya Peninsula toward Nicaragua, where the dry season (November to May or June, MAP 1000–1500 mm) is augmented by local slope, exposure, drying winds, and edaphic conditions. The highest canopy is 20–30 m tall, the subcanopy is 10–20 m tall, most trees are semi-deciduous, and there is a prominent legume component. Remnants of the forest are preserved in the Santa Rosa National Park (Fig. 3.88) and at Palo Verde in northwestern Costa Rica. Savanna-like communities are found on the upper plateau of Santa Rosa National Park, but illustrating the point that natural savannas are not a prominent part of the Central American vegetation, the grass (*Hyparrhenia rufa*) is an introduction from Africa and burning is required to keep the vegetation from returning to an oak woodland.

Aquatic vegetation in Costa Rica consists of ~500 species including *Ceratopteris pteridoides* (Figs. 3.89–3.91), which is frequent in the fossil record of Latin America (Appendices 2.1, 2.2). The mangrove formation consists of *Avicennia*, *Conocarpus*, *Laguncularia*, and *Rhizophora*, along with *Pelliciera rhizophorae* (Fig. 3.92), which grows along the Santa Elena Peninsula of northwestern Costa Rica.

The lowland Neotropical rain forest (Figs. 3.93, 3.94) is a tall assemblage with *Minquartia guianensis* (45–55 m) and *Ceiba pentandra*, and it is the most species-rich plant formation in Costa Rica. It grows in areas characterized by mean annual daily temperatures between 18° and 24° C, more diurnal temperature variation than seasonal, and MAP exceeding 2000 mm and no

Figure 3.94. Cleared forest, Guatemala. Photograph by Bruce Graham.

month with less than 100 mm (Sanford et al., 1994, p. 19). By this definition, the vegetation of the Amazon and Orinoco basins of South America, the lowlands of Central America, and a small extension into southeastern Veracruz, Mexico, qualify as tropical rain forest. The formation is extensively developed on the southwest Pacific side of Costa Rica, where rainfall reaches 5000 mm. One expanse in the vicinity of the Golfo Dulce is well known through an early study by Allen (1956). Rain forest also occurs in the lowlands on the wetter Atlantic side between Panama and Nicaragua where rainfall may exceed 6000 mm. The affinities of the forest are with South America, and the wettest parts are especially similar to the vegetation of the Chocó region of Colombia. Genera common to both areas are *Anthodiscus*, *Batocarpus*, *Caryocar*, *Chaunochiton*, *Couratari*, *Cremastosperma*, *Huberodendron*, *Parkia*, *Peltogyne*, *Uribea*, and *Vantanea*. Other prominent components of the lowland tropical rain forest in Costa Rica are given in Appendix 1.13.

The lower to upper montane broad-leaved forest includes the Holdridge life zones of tropical moist forest (the most extensive life zone in Costa Rica; the palm *Scheelea* [*Attalea*] *rostrata* is abundant, and drip-tips are common), tropical premontane moist forest (through tropical premontane rain forest, ~equal cloud forest), tropical premontane wet forest, tropical premontane rain forest, tropical lower montane moist forest (*Quercus* with gnarled trunks abundant; elfin forest), tropical lower montane wet forest, tropical lower montane rain forest, tropical montane wet forest, and tropical montane rain forest. A bog community of *Puya dasylirioides*, an *Alnus* (alder) association, and an open-disturbed seral phase with *Cecropia* are illustrated in Figs. 3.95–3.97. The Holdridge system, like those used for the selvas of Mexico, subdivides the extant broad-leaved community between the lowland rain forest and the páramo into far more types than can be discerned in fossil assemblages. Unless a combination of genera or a set of morphological features (drip-tips, leaf-size categories, numerous lianas or epiphytes) identifies a specific association, the paleocommunity is referred to as the lower- to upper-montane broad-leaved forest.

Figure 3.95. Puya bog (*Puya dasylirioides*), Cordillera de Talamanca, Costa Rica. Other plants include *Blechnum buchtienii*, *Chusquea*, *Escallonia poasana*, and *Vaccinium consanguineum*. Photograph by Sally Horn.

Figure 3.96. *Alnus acuminata* along Interamerican Highway, Cordillera de Talamanca, Costa Rica. Photograph by Sally Horn.

Figure 3.97. *Cecropia obtusifolia*, Corcovado National Park, Costa Rica. Photograph by Sally Horn.

The general composition of this forest at Monteverde in Costa Rica, with transitions to the wetter lowland tropical rain forest and drier upland forests, is given in Appendix 1.14 (Haber, 2000; Haber et al., 1996). With reference to the cloud forest association, Standley (1937–1938) described the setting as "…drenched every night and sometimes all day with drizzling rain or heavy downpours, and much of the time…by drifting clouds." A difference between the high-altitude forests of Costa Rica, and those of Mexico and Guatemala, is that the former are dominated by oaks (e.g., on Cerro de la Muerte, 3100 m; and on Cerro Chirripó, near 3800 m) and the latter are dominated by pines and oaks or by pines and fir at the very highest elevations. A difference in the paleocommunities is that *Picea* (spruce) was frequently a member of the high montane forests of Mexico and Guatemala during the Neogene, but it is not known in the fossil record of southern Central America.

New discoveries of plants and animals at the genus and even the family level continue to be made from Latin America where habitats are preserved. An example is *Ticodendron* in the Reserva Forestal de San Ramón, Alajuela Province (*T. incognitum*, Gómez-Laurito & Gómez, 1989; Zamora et al., 2004a, b). It was long overlooked because it resembles *Alnus*, with which it grows (Hammel & Burger, 1991), but it is now placed in the Central American endemic monotypic family Ticodendraceae in the order Fagales (Gómez-Laurito & Gómez, 1991). *Ticodendron incognitum* is now known from southern Mexico (Oaxaca) to central Panama (Bocas del Toro, Chiriquí, and Coclé provinces) at elevations between 500 and 2400 m in cloud forests. Once the distinctive features of single-toothed leaf margins, drupaceous fruits, four-loculed ovary, and hemitropous ovules

Figure 3.98. *Pteris deflexa*, Pedregal Esquilón, Veracruz, Mexico. From Tryon and Tryon (1982; photograph by Walter Hodge). Used with permission of Springer Verlag, Berlin.

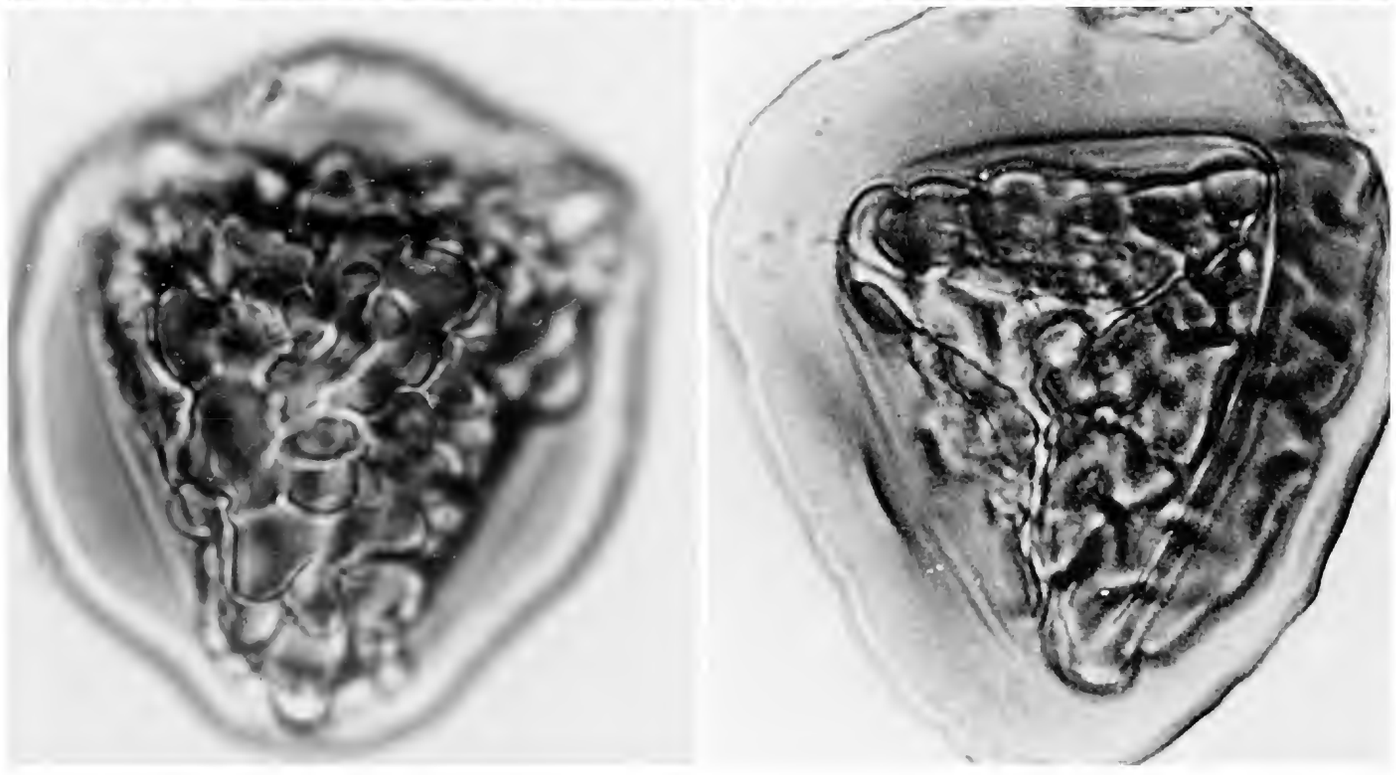


Figure 3.99 (left). Modern spore of *Pteris quadriaurita*.

Figure 3.100 (right). Fossil spore of *Pteris* from the Miocene La Boca Formation, former Canal Zone, Panama.

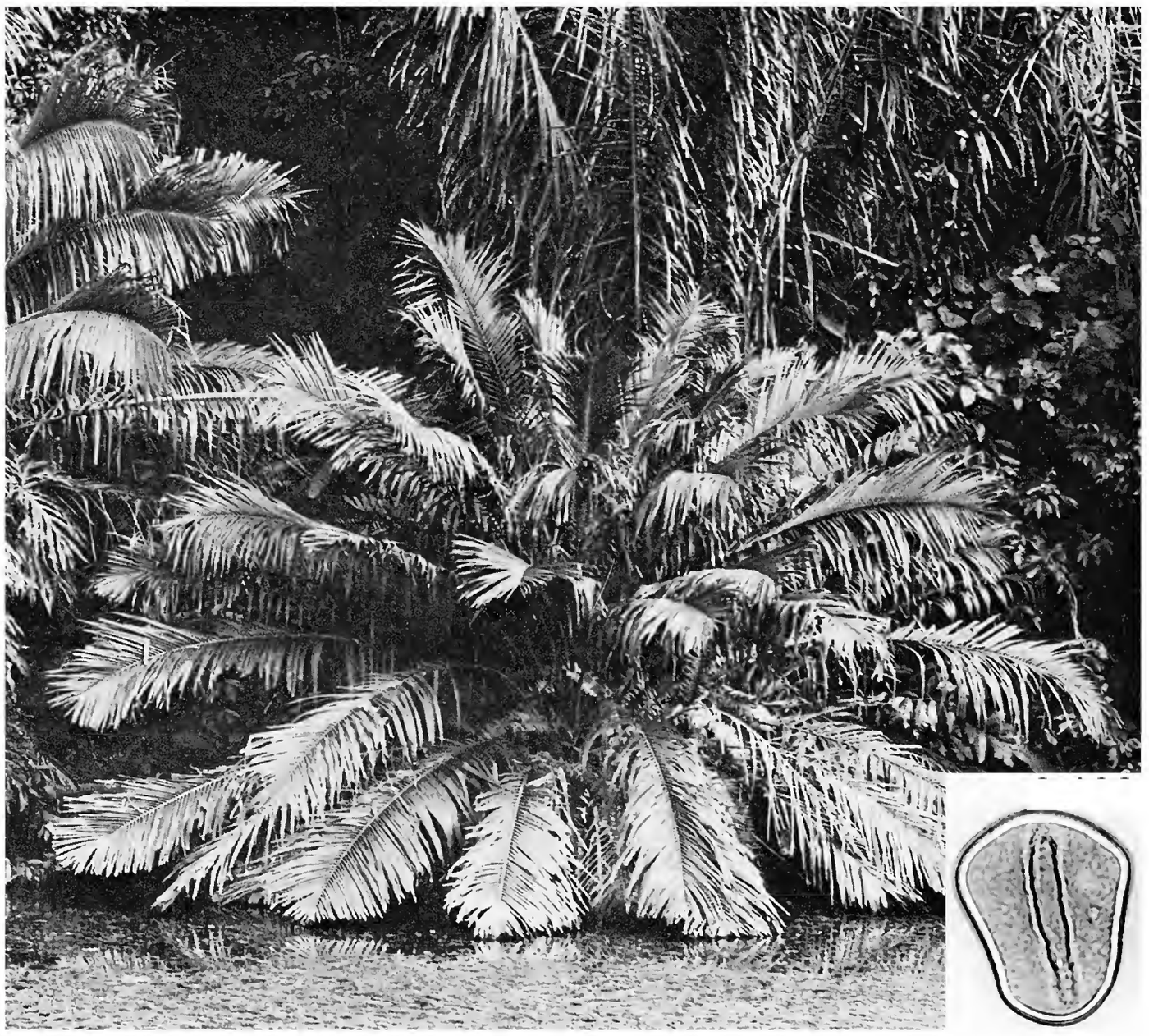


Figure 3.101. *Elaeis* (*Corozo*) *oleifera*, Barro Colorado Island, Panama. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.

Figure 3.102 (inset). Modern pollen of *Elaeis* (*Corozo*) *oleifera*.

Figure 3.103. *Acacia riparia*, Barro Colorado Island, Panama. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.

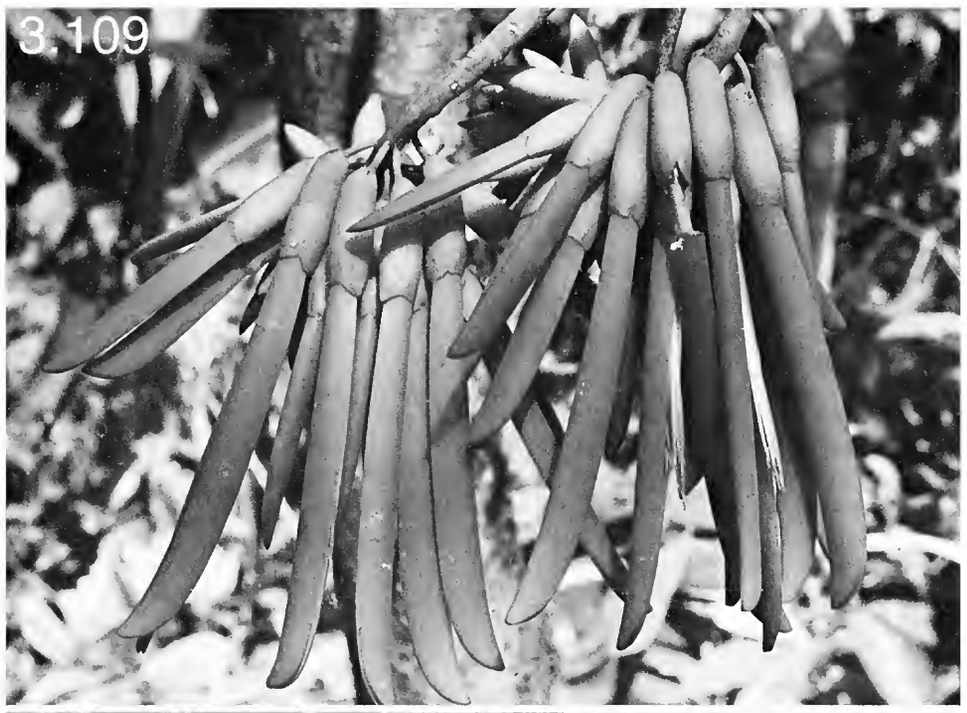
became known, fossil leaf and fruit collections were re-examined for specimens with these features. Both leaves and fruits of *Ticodendron*, or with *Ticodendron* affinities, have been found in North America (*Ferrignocarpum* from the middle-late Eocene Clarno flora of Oregon; fruits about one-third the size of *Ticodendron*) and Europe (*Carpolithus* sp. 38 from the early Eocene London Clay flora of England; Steven Manchester, Susanne Renner, pers. comm., 2005). Fossils of *Ticodendron* have not been found in Latin America (the pollen is similar to *Carpinus* and *Corylus* of the Betulaceae), but it, or its progenitor, apparently is another amentiferous woody genus like *Alfaroa* and *Oreomunnea* that migrated from the north or differentiated in the temperate cloud forests of Mexico and Central America. Another example is *Trigonobalanus*, discovered in the Andean forests of South America (see Chapter 3, Colombia).

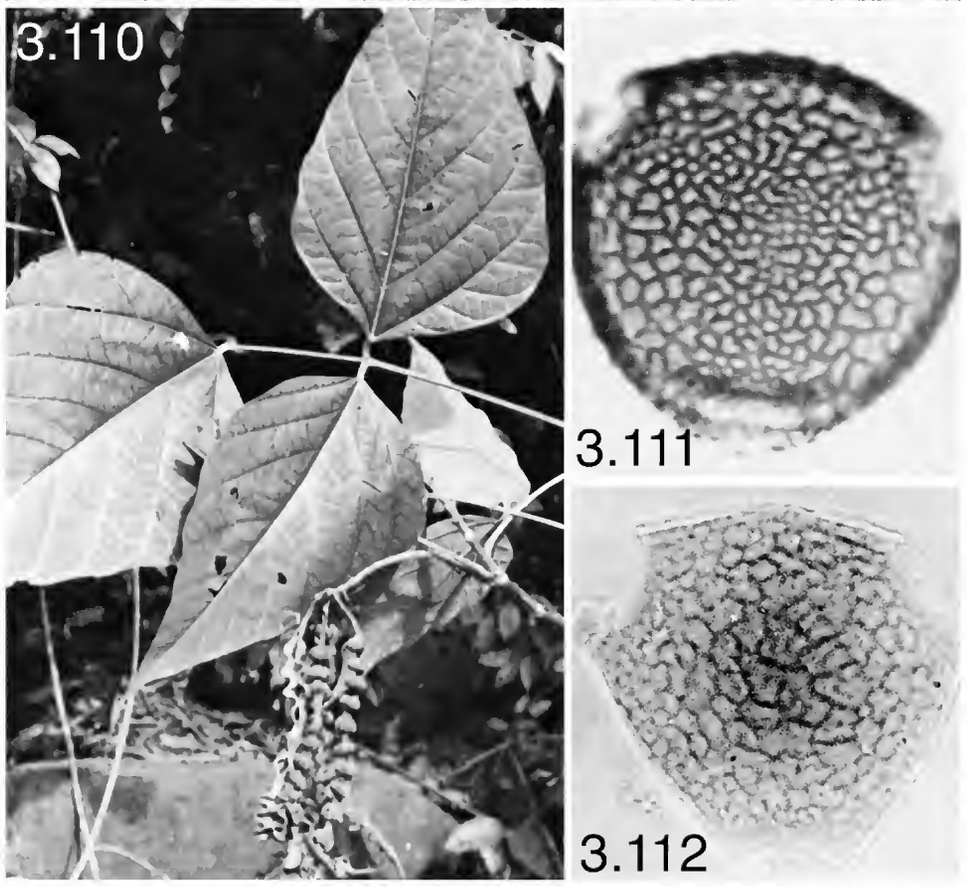
The relationship of the primarily shrubby páramo in Central America (Kappelle & Horn, 2005) is with the high Andes (Weber, 1958; Cleef & Chaverri P., 1992). About 95% of the vascular plant genera and ~50% of the species are the same. In contrast, the relationships of the primarily herbaceous Mexican–Guatemalan páramo are with the temperate and Holarctic (northern) tundra. Treeless vegetation above timberline in Costa Rica occurs in the cold humid environment of Cerro Chirripó and Cerro de la Muerte in the Cordillera de Talamanca. Frosts are common and there are anecdotal reports of snow. Endemics in the Talamanca region of Costa Rica and Panama include *Iltisia* and *Westoniella*, northern elements at or

Figure 3.104. *Combretum decandrum*, Barro Colorado Island, Panama. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.

Figures 3.105 (inset left), 3.106 (inset right). Modern pollen of *Combretum fruticosum* (equatorial and polar view).

Figures 3.107 (left), 3.108 (right). *Terminalia amazonia*, Barro Colorado Island, Panama. 3.107—Habitat. 3.108—Flowers and leaves. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.





Figures 3.109, 3.110. *Erythrina costaricensis*, Barro Colorado Island, Panama. 3.109—Flowers. 3.110—Leaves. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.

Figure 3.111. Modern pollen of *Erythrina panamensis*, polar view.

Figure 3.112. Fossil pollen of *Erythrina*, Miocene Gatún Formation, former Canal Zone, Panama.

near their southernmost distribution are *Cirsium*, *Comarostaphylis*, *Garrya*, *Helianthemum*, and *Mahonia*, and southern elements at or near their northernmost distribution are *Aciachne*, *Diplostephium*, *Gaiadendron*, *Lorenzochloa* (*Ortachne*), and *Niphogeton*.

Panama

The earliest flora of Panama was written by Seemann (1854), followed by treatments for local areas. Some of these are Barro Colorado Island (Standley, 1927; Croat, 1978; Gentry, 1990; Hubbell & Foster, 1990; see *Pteris* [Figs. 3.98–3.100], *Elaeis* [*Corozo*] *oleifera* [Figs. 3.101, 3.102], *Acacia* [Fig. 3.103], *Bauhinia*, *Cassia*, *Combretum* [Figs. 3.104–3.106], *Erythrina* [Figs. 3.109–3.112], *Faramea* [Figs. 3.113–3.115], *Sapium*, *Terminalia*

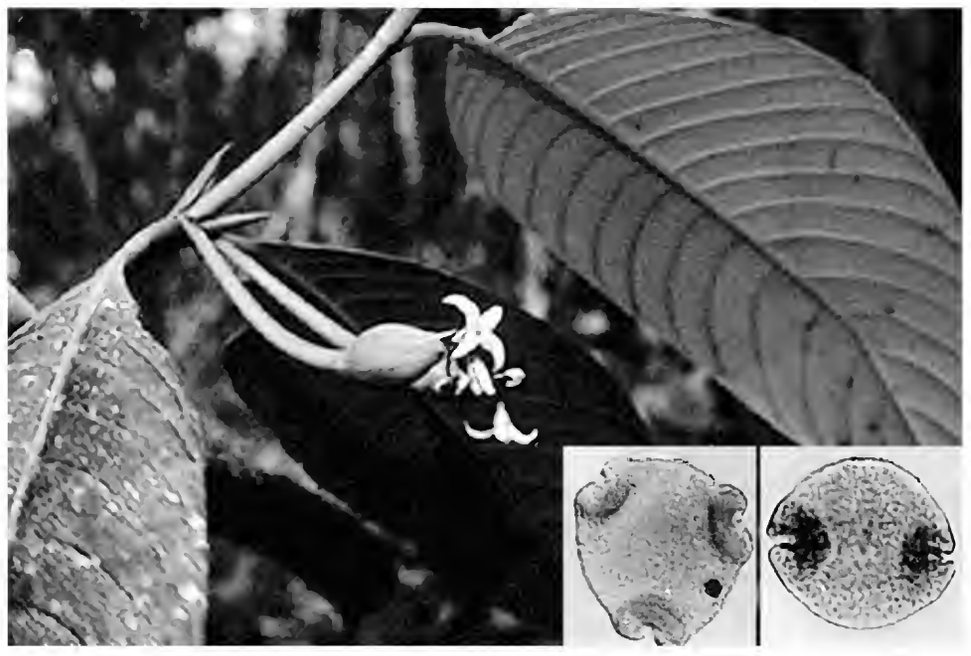


Figure 3.113. Flowers and leaves of *Faramea*, Cerro Jefe, Panama. From TROPICOS, photograph by Alwyn Gentry. Used with permission of the Missouri Botanical Garden, St. Louis.

Figure 3.114 (inset left). Fossil pollen of *Faramea* from the Miocene Gatún Formation, former Canal Zone, Panama, triporate form.

Figure 3.115 (inset right). Fossil pollen of *Faramea* from the middle to late Eocene Gatuncillo Formation, Panama, diporate form.

[Figs. 3.107, 3.108], *Tournefortia* [Fig. 3.116]), the former Canal Zone (Standley, 1928), San José Island (Johnston, 1949), the Golfo Dulce (Allen, 1956; see *Ceiba pentandra*, Fig. 3.117), and a general review of the vegetation by Porter (1973). There is a comprehensive flora of Panama by Woodson (1943–1981), updated by D'Arcy (1987), and its completion was commemorated by a volume on the natural history of Panama (D'Arcy & Correa A., 1985). The Smithsonian Tropical Research Institute's (STRI) field laboratory on Barro Colorado Island, established in 1923, has been the site of numerous other studies on the tropical biology of the country (e.g., see papers in Condit, 1998; Leigh et al., 1996; Leigh, 1999; and Roubik & Moreno P., 1991, on the spores and pollen).

The strategic and economic importance of the Panama Canal and the presence of STRI (Pennisi, 2001) have provided facilities for research in Panama for nearly a century. As a result, a considerable amount of information has been generated, including a number of vegetation maps, although several show Panama as part of broader outline maps of Latin America and background for study of the fauna, or are highly generalized sketches of the major plant formations. Those dealing with Panama specifically include Goldman (1920), Goldman and Zetek (1926), Platt (1938), Schery (1942), Garver (1947), Holdridge and Budowski (1956, 1959), Bennett (1968), and Myers (1969). There are also regional maps of eastern Panama (Lamb, 1953; Golley et al., 1969; Viksne et al., 1970), San José Island (Erlanson, 1946; Johnston, 1949), Barro Colorado Island (Park et al., 1940; Bennett, 1963), Ft. Sherman and Ft. Gulick (Wiley et al., 1955), and the Darién Province (Duke & Porter, 1970; *Cavanillesia*, Figs. 3.119–3.122; *Cupania*, Fig. 3.123; *Prioria* and *Pterocarpus*, Fig. 3.118). In the Holdridge classification, the vegetation of Panama is sorted into eight life zones (Holdridge &

Figure 3.116. *Tournefortia angustiflora*, Barro Colorado Island, Panama. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.

Figure 3.117. *Ceiba pentandra* near Palmar, Golfo Dulce, Costa Rica. From Allen (1956). Reprinted with permission of the University Press of Florida, Gainesville.

Figure 3.118. Lowland Neotropical rain forest in swamps of the Darién, Panama. Buttressed trees are *Pterocarpus officinalis*, and the non-buttressed trees in the foreground are *Prioria copaifera*. From Hartshorn (2000). Reprinted with the permission of Cambridge University Press.

Figure 3.119. *Cavanillesia platanifolia*, Panama. From TROPICOS, photograph by Barry Hammel. Used with permission of the Missouri Botanical Garden, St. Louis.

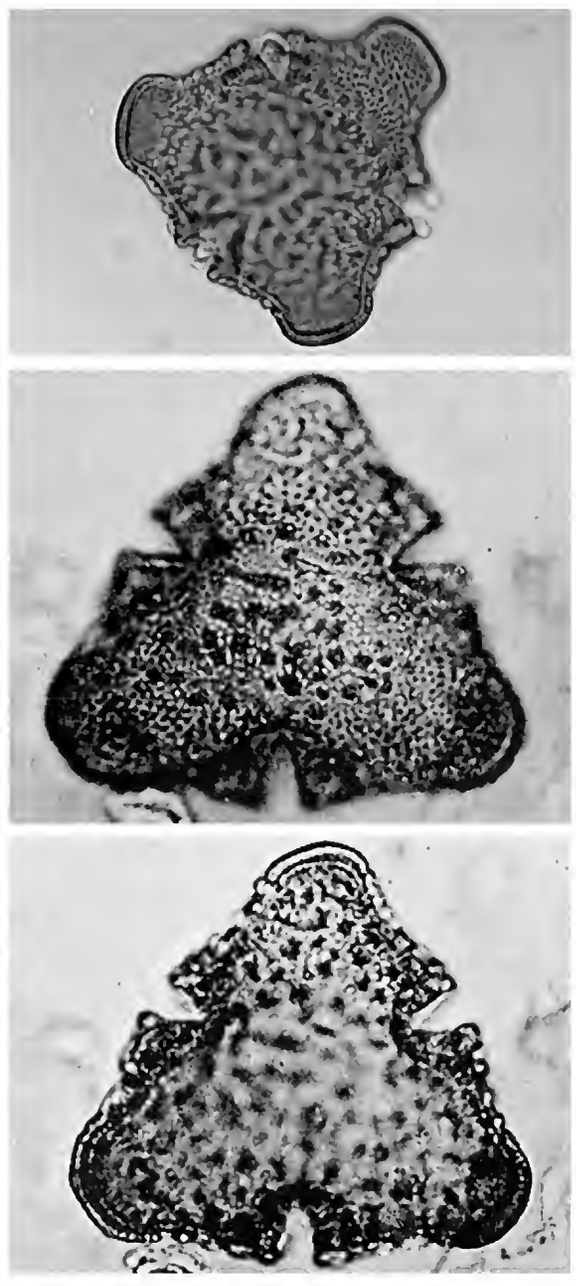


Figure 3.120. Modern pollen of *Cavanillesia platanifolia*.

Figures 3.121 (center), 3.122 (bottom). Fossil pollen of *Cavanillesia* from the Quaternary of Panama. Photographs by Alan Graham, from Bartlett and Barghoorn (1973).

Figure 3.123. Fruits and leaves of *Cupania* from the Cerro Azul, Panama. From TROPICOS, photograph by Alwyn Gentry. Used with permission of the Missouri Botanical Garden, St. Louis.

Budowski, 1956; Fig. 3.125). These are listed in Appendix 1.15 and arranged according to the system used here.

There are several aspects of modern Panamanian vegetation that are a result of geologic events and that can be assessed from the plant fossil record. One is that the Pacific (southern) side of Panama is generally drier than the Atlantic (northern) side. The principal reason is the presence of the Cordillera Central, which diverts some of the moist air coming off the Atlantic Ocean via the northeast trade winds. Another is that the few northern temperate elements in southern Central America (e.g., *Quercus*) mostly grow in the uplands (Fig. 3.124). Thus, the initial presence of drier vegetation and northern temperate elements should correspond approximately to the uplift of the Cordillera Central. This is the record revealed by the plant fossil record, and it is reviewed in Chapter 6.

Figure 3.124. Cloud forest (montane broad-leaved forest), Cerro Tuté, Panama. Photograph by Scott Mori.

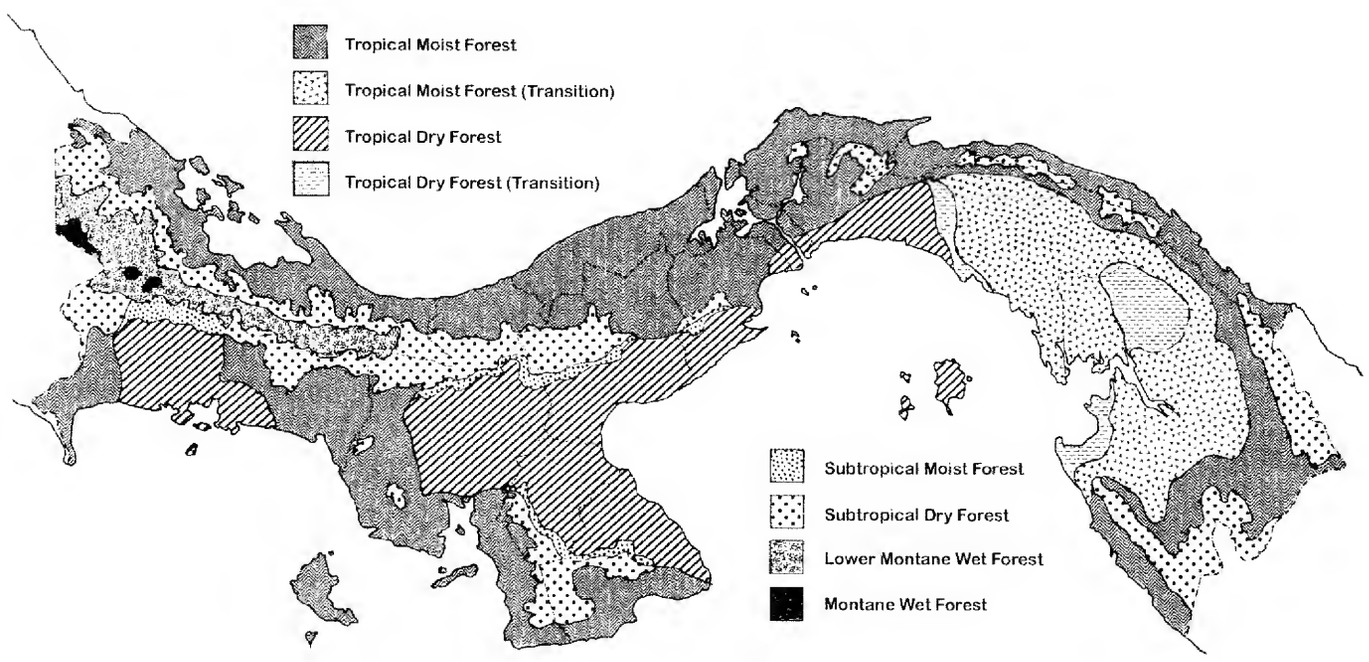


Figure 3.125. Life zones of Panama. Map by Alan Graham, from Porter (1973) based on Holdridge and Budowski (1956).

SOUTH AMERICA

A guess as to the number of vascular plant species in South America is ~125,000, or about six times that in North America north of Mexico (I: p. vii). The most extensive flora in the north temperate region is in the People's Republic of China with ~31,000 species. Whatever the eventual number, Neotropical plant diversity is vast, and only the broadest generalizations can be made about the plant formations and their composition, distribution, ecology, and the range of climates under which they grow. In discussing the vegetation of South America, the criteria established earlier are followed; namely, a classification system that is appropriate to a summary of vegetation history; primary consideration given to those plant formations, associations, and phases potentially recognizable in the fossil record; and emphasis placed on those countries, plant formations, and times for which sufficient paleobotanical data exist to address questions of paleoecology and ecosystem evolution. Individual lineages are discussed in Chapter 8, and an inventory of fossil plant taxa is given in Appendix 2. The sequence of countries discussed is the same as in previous chapters—the Andean countries of Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, and Argentina, and the Amazon Basin country of Brazil. Others (the Guianas, Paraguay, and Uruguay) are mentioned briefly because limited information is available on their vegetation history.

Vegetation maps of South America have been published by Ab'Saber (1977), Hueck and Seibert (1972), Haack (1985), and UNESCO (1980–1981) with the largest scale (1:5,000,000) and utilizing the satellite images of Landsat 1 and 2 (1973–1976; Multispectral Scanner, spectral channel No. 5 [MSS5]). The Hueck and Seibert (1972) map shows the potential natural vegetation, while the UNESCO (1980–1981) version used here shows the actual existing vegetation including degraded plant formations and croplands. A soils map has been published for South America (UNESCO–FAO, 1975; see also the climate maps of Haack [1985]). Cloud forests for countries of South America are discussed in Kappelle and Brown (2001), who include a list of forest preserves where remnants of this and other vegetation types are somewhat protected. There is also a review of the lowland vegetation of tropical South America (Daly & Mitchell, 2000).

The UNESCO map includes 103 communities, and among these the nontropical lowland region alone is subdivided into 14 types, and there are 15 additional edaphic formations. This classification is shown in Table 3.7, the more general one followed here is shown in Table 3.8 (with the approximately equivalent UNESCO units), and an index map is given in Fig. 3.126. Maps for individual countries are mentioned at appropriate places in the text, and others are included in the bibliography in the Additional References section at the end of this chapter.

Study of the UNESCO map reveals several points of interest, and others appear on the larger-scale maps for individual countries. For example, the Amazon Basin is shown as covered uniformly by lowland tropical rain forest (No. 8 on Fig. 3.126). Actually, only about one-half of the basin consists of this plant formation. There is a mosaic of vegetation types, including riverine communities, those affected to varying degrees by the tidal influx of brackish waters, others that are inundated by freshwater during the rainy season, and numerous stratified communities occupying microhabitats among the tall forest trees. Edaphic control is prominent, there are grasslands and savannas where fire is common, and caatingas and cerrado surround the basin (No. 2 on Fig. 3.126). This setting allows for the relatively rapid exchange of wet and dry elements during cold-dry and warm-moist geologic intervals.

Another pattern, particularly responsive to climatic change, is the altitudinally zoned vegetation on the slopes of the Andes Mountains where the communities are stressed along steep gradients from the lowlands to the high-altitude páramo and puna (e.g., Nos. 12 and 9 on Fig. 3.126). In this setting, slight changes in temperature and rainfall produce significant shifts in ecotones that are recorded by plant microfossil assemblages preserved in lakes and bogs along the slopes. These data are pertinent to questions about the time of origin of the páramo and, by implication, the uplift history of the Andes Mountains, the unsettled question of the origin of the different páramo associations (e.g., grassy páramo), and whether these are natural or anthropogenic. Other information from progressively lower-altitude sites and from the basin floor are relevant to the question of whether tropical biotas and environments were generally stable during the late Cenozoic, as suggested in the older literature and by more recent results from the CLIMAP project, or whether they fluctuated over time (Chapters 7, 8).

Another site on the map that attracts attention is the very low-lying, almost sea-level landscape and associated lowland Neotropical rain forest in the Atrato (Colombia)–Darién (Panama) region. Slight changes in sea level and vertical movement of the land would connect-disconnect North and South America through this region. Relative sea level was higher than at present by up to 300 m during the Cretaceous, was lower by 100–121 m at the LGM at 18 Kyr, and is estimated to rise at a rate of ~0.2–1 m/100 yr for the near future due to a temperature rise of ~4°–5° C by the year 2100, glacial melting, and the thermal expansion of ocean waters. This history has obvious implications for the exchange of biotas between North and South America during Late Cretaceous and Cenozoic times (Chapters 6, 8).

An additional feature of interest on the map is the pronounced arid zone along the Pacific coast of South America from ~6°S to ~29°S. Extreme habitats are susceptible to magnified responses from fluctuations in climate and in the physical environment. Given the evidence for diverse and rapid en-

Figure 3.126 (facing page). General index map of South American plant formations based on UNESCO (1980–1981). Some vegetation types of scattered and limited extent are not shown (viz., 5–beach/strand/dune; 7–aquatic); large extents of cultivated/disturbed vegetation are designated C/D (e.g., east coast from ~4°N to ~30°S + the Pampas; west coast from ~10°N, Maracaibo Basin region, through the Puna and adjacent regions to ~30°S), and those of smaller extent are included in the immediately surrounding natural plant formation. Letters/numbers/symbols in parentheses refer to those on the more detailed UNESCO map.

1. Desert (D)
2. Shrubland/chaparral–woodland–savanna
   - 2a. Seasonal forest (5)
   - 2b. Subhumid grassland with woody species (13)
   - 2c. Thorn-forest with succulents (18)
   - 2d. Deciduous forest and "cerrado" (10)
   - 2e. Drought-deciduous woodland and "chaco" (17)
   - 2f. Deciduous woodland (22)
   - 2g. Grassland with woody species; generic and species composition different from 2b (38)
   - 2h. Deciduous scrub (61)
   - 2i. Semi-deciduous shrubland (67)
   - 2j. Deciduous open shrubland (85)
   - 2k. Subpolar deciduous shrubland (84)
   - 2l. Subdesert thorn-scrub (65)
   - 2m. Evergreen shrubland (66)
   - 2n. Subdesert thorn-scrub (67)
3. Grassland (57)
   - 3a. Flooded grassland, pantanal (101)
   - 3b. Grassland with palms (99)
   - 3c. Grassland with woody species (96)
   - 3d. Pampas (∀)
   - 3e. Grassland grading upward toward Andean meadows
4. Mangrove (94)
6. Freshwater bog/marsh/swamp (90)
8. Lowland tropical rain forest (1, 2; including 89—riparian forest)
9. Evergreen submontane forest (32)
   - 9a, c. Ombrophillous submontane forest grading upward into montane forest (29)
   - 9b. Broad-leaved forest (77)
   - 9d. Subpolar forest (76)
   - 9e. Subpolar swamp forest (82)
   - 9f. Valdivian forest (78)
10. Submontane forest grading into higher altitude montane forest
11. Meadow of higher latitudes (86, 87)
12. Andean meadow of higher latitudes (88)
    - 12a. páramo, puna (86)

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vironmental change at the low latitudes during the Cenozoic, it can be anticipated that deserts in western South America, like their counterparts in northern Mexico and the southwestern United States, have had a complex and dynamic history.

The vegetation summary begins with Venezuela and introduces the terminology, classification, and composition of the plant formations used for South America. Selected communities from other countries are discussed where they provide especially good examples of a particular ecosystem, or where they have been the subject of extensive ecological and paleoecological research. These communities and countries are:

Desert
- Chile (and in Appendix 1.22)

Shrubland/chaparral–woodland–savanna
- Venezuela (Appendix 1.17)
- Chile (Appendix 1.22)
- Bolivia (Appendix 1.21)
- Argentina (Appendix 1.23, Gran Chaco, Monte, chaqueña)
- Brazil (Appendix 1.25, cerrado, caatingas; mata seca or semi-decídua on shallow soil; estacional on deep soil with *Cavanillesia* common; dry deciduous forest on calcareous limestone)

Grassland
- Argentina (Appendix 1.23, Pampas)

Freshwater herbaceous bog/marsh/swamp
- Brazil (Appendix 1.26, pantanal)

Lowland Neotropical rain forest
- Venezuela (Orinoco River delta)
- Colombia (chocó)
- Brazil (Amazonian and Atlantic forests, várzea; Appendix 1.27)

Lower to upper montane broad-leaved forest
- Venezuela (Appendix 1.17)
- Ecuador (Appendix 1.20)
- Bolivia (Appendix 1.21)
- Argentina (Appendix 1.23, yungas)

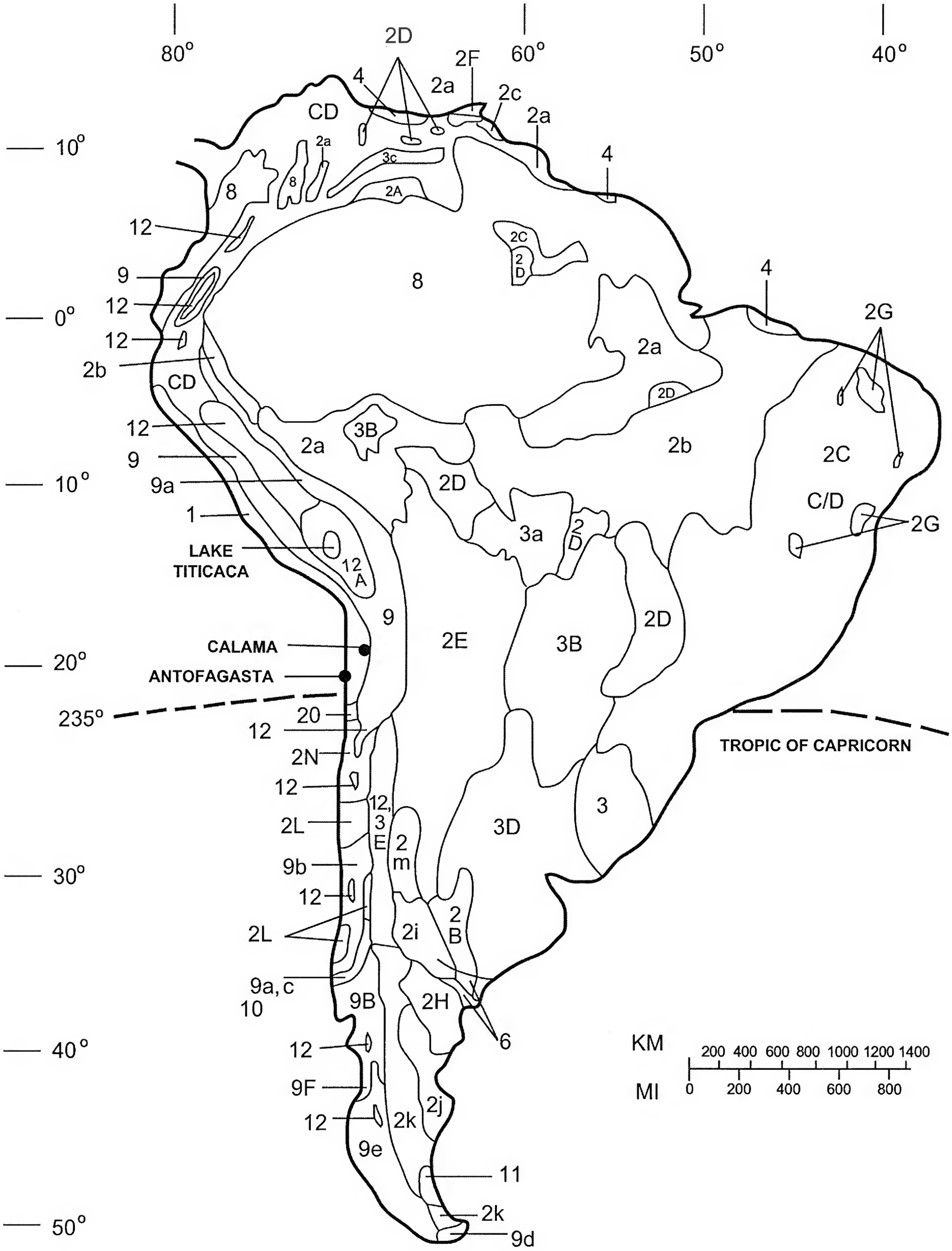
Alpine tundra (páramo/puna)
- Colombia (Appendix 1.19)

Tundra
- Argentina (Appendix 1.23)

Venezuela

The vegetation of Venezuela is summarized by Ewel et al. (1976) following the Holdridge life zone classification. The 19 zones recognized for the country are correlated with the plant formations used in the present text in Appendix 1.17, and a generalized index map of the vegetation is shown in Fig. 3.127. More specific areas studied in detail include Ávila (Steyermark & Huber, 1978), the Guayana–Llanos ecotone (Boom, 1990), sinkholes in the Meseta de Sarisariñama (state of Bolívar; Carias & Steyermark, 1976), Guaramacal National Park (Dorr et al., 2000), the Guayana Highlands (Maguire, 1970, 1979; Maguire et al., 1953 et seq.), and the Venezuelan Guayana comprising ~10,000 vascular plant species over the 454,000 km^2 (Steyermark et al., 1995 et seq.) area. The last includes a vegetation map of the region based on Huber and Alarcón (1988).

Desert—The only parts of Venezuela that qualify as desert are narrow zones along the coasts of the La Guajira Peninsula and Paraguaná Peninsula bordering the Golfo de Venezuela (Fig. 3.128). The elevation is from sea level to ~100 m, MAT


80°
60°
50°
40°
10°
0°
10°
20°
30°
40°
50°
235°
2D
2F
4
2a
2c
CD
3c
2A
8
12
9
2b
9a
1
LAKE TITICACA
CALAMA
ANTOFAGASTA
20
2N
2L
9b
9a, c
10
9F
11
2k
9d
2C
3B
3a
3D
3
2E
2G
C/D
2i
2j
2H
6
9e
9B
TROPIC OF CAPRICORN
KM
200 400 600 800 1000 1200 1400
MI
0 200 400 600 800

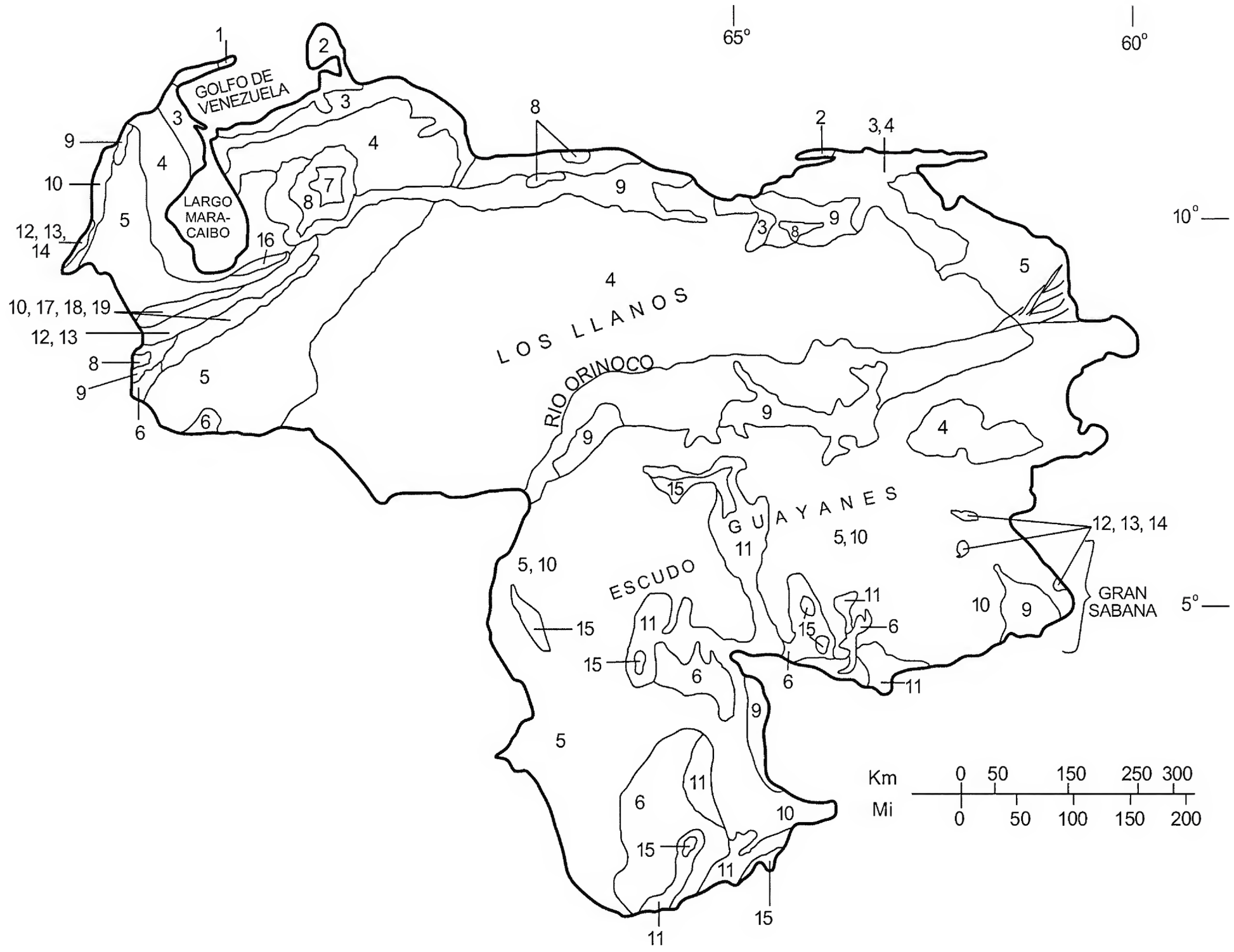


Figure 3.127. General index map of the principal plant formations of Venezuela (based on Ewel et al., 1976). See Appendix 1.17 for index to plant formation names and representative species.

is ~25° C, and MAP is 125–250 mm. The combination of coastal winds and warm temperatures creates a high evapotranspiration potential that, along with low rainfall, produces a desert environment. Parts of the landscape are almost devoid of plant cover, while moister sites support *Cercidium praecox*, *Prosopis juliflora*, and the cacti *Lemaireocereus*, *Mammillaria*, and *Opuntia*, all familiar from the deserts of Mexico.

Shrubland/chaparral–woodland–savanna—Northern Venezuela is mostly dry tropical forest (bosque seco tropical; No. 4 in Fig. 3.127, Fig. 3.129) with drier vegetation growing along the northern coast (Nos. 2, 3, 7, 8 in Fig. 3.127). This plant formation extends from ~300 to 1500 m, but the upper limit is around the capital of Caracas, where the land is disturbed and the vegetation is highly modified. The MAT is 18°–29° C, with the cooler temperatures in the premontane regions, and the MAP is 250–1800 mm, with the extremes at the transition between the desert and the lower to upper montane broad-leaved forest. The genera characteristic of the shrubland/chaparral–woodland–savanna in Venezuela include *Agave*, *Aristida*, *Bromelia*, *Bulnesia*, *Capparis*, *Castela*, *Cercidium*, *Chrysobalanus*, *Copaifera*, *Curatella*, *Lippia*, *Opuntia*, *Pereskia*, *Pithecellobium*, *Platymiscium*, *Pterocarpus*, and *Tabebuia*.

Neotropical savannas (Gran Sabana, Venezuela)—There is an extensive literature on Neotropical savannas (Beard, 1953; Heyligers, 1963; Blydenstein, 1967; van Donselaar, 1969; Teunissen & Wildschut, 1970; Talbot & Kesel, 1975; Eiten, 1982; Huntley & Walker, 1982; Bourliére, 1983; Sarmiento, 1983; Walker, 1987; Haase & Beck, 1989; Medina & Silva, 1990; Duivenvoorden & Cleef, 1994; Prance, 1996). Nonetheless, understanding the origin and current status of savanna vegetation in tropical America is complicated by several factors. One is that the economic potential of the ecosystem promotes expansion through clearing of adjacent forests and intense modification through agriculture and grazing, and this has been the case for millennia. Another is that overuse converts savannas into near-deserts through desertification, a process that is affecting savannas, grasslands, and deserts on a global scale. The environments of these communities are not conducive to the widespread preservation of plant remains, and their reconstruction from fossil pollen assemblages is

Table 3.7. Vegetation types of South America according to UNESCO (1980–1981). Numbers are those used on the UNESCO map to designate vegetation types.

Climatic Formations

I. Constantly warm regions

Extremely moist and very moist formations (MAP >2000 mm)

1. Extremely moist forest (MAP >3000 mm) 2. Very moist forest (MAP >2000 mm)
3. Degraded formations + crops 4. Grassland with woody species

Moist formations (MAP 1000–2000 mm)

Continental types

5. Seasonal forest 6. Degraded formations + crops 7. Grassland with woody species

Coastal types

8. Evergreen lowland forest 9. Degraded formations + crops

Subhumid formation (MAP 1000–2000 mm)

10. Deciduous forest and "cerrado" 11. Xeromorphic forest 12. Degraded formations + crops
13. Grassland with woody species 14. Grassland

Dry formations (MAP 500–1000 mm)

15. Xeromorphic woodland 16. Woodland with succulents 17. Drought-deciduous woodland and "chaco" 18. Thorn-forest with succulents
19. Semi-deciduous forest 20. Degraded formations + crops

Very dry formations (MAP <200 mm)

21. Woodland with succulents 22. Deciduous woodland 23. Deciduous thicket with succulents
24. Deciduous thicket without succulents 25. Degraded formations + crops

Arid formations (MAP <200 mm)

26. Dwarf-shrubland with succulents 27. Degraded formations + crops

II. Regions with a cool season

a. Tropical submontane regions

Extremely moist and very moist formations (MAP >2000 mm)

28. Extremely moist submontane forest 29. Ombrophilous (very wet) submontane forest 30. Degraded formations + crops

Moist formations (MAP 1000–2000 mm)

31. Atlantic forest 32. Evergreen submontane forest 33. Forest with *Podocarpus* 34. Degraded formations + crops

Subhumid formations (MAP 1000–1500 mm)

35. Semi-deciduous forest and "cerradão" 36. Thorn forest 37. Degraded formations + crops 38. Grassland with woody species

Dry and very dry formations (MAP 200–1000 mm)

39. Dry forest 40. Thorn woodland 41. Submontane thicket and "caatinga" 42. Deciduous scrub 43. Degraded formations + crops

b. Tropical montane regions (MAP 2000–3000 mm)

Very moist formations (MAP >2000 mm)

44. Montane forest 45. Degraded formations + crops

Moist and subhumid formations (MAP 2000–1500 mm)

46. Cloud forest 47. Moist seasonal montane forest 48. Degraded formations + crops
49. Subhumid montane forest 50. Degraded formations + crops

Dry formations (MAP 500–1000 mm)

51. Deciduous montane forest 52. Montane deciduous scrub 53. Degraded scrub + crops

c. Nontropical lowland regions

54. Forest with *Araucaria* 55. Subtropical forest and "cerradão" 56. Grassland with woody species 57. Grassland 58. Deciduous forest
59. Degraded formations + crops 60. Sclerophyllous woodland 61. Deciduous scrub 62. Sclerophyllous thicket 63. Grassland (pampa)
64. Xeromorphic woodland 65. Subdesert thorn-scrub 66. Evergreen shrubland 67. Semi-deciduous shrubland

III. Cold regions

a. Andean high mountain regions

68. Páramo with woody species 69. Páramo 70. Degraded páramo 71. Moist puna
72. Degraded moist puna 73. Puna 74. Degraded puna 75. Dry puna

b. Lowland regions

Very moist formations (MAP >2000 mm)

76. Subpolar forest 77. Broad-leaved forest 78. Valdivian forest 79. Degraded formations + crops

Moist formations (MAP 1000–2000 mm)

80. *Araucaria* forest 81. Deciduous forest 82. Subpolar swamp forest 83. Degraded formations + crops

Dry formations (MAP 500–1000 mm)

84. Subpolar deciduous shrubland

Very dry formations (MAP 200–500 mm)

85. Deciduous open shrubland

IV. Very cold regions

86. Tundra 87. Bunch-grass community 88. Andine meadow of higher latitudes

Edaphic Formations

89. Riparian (gallery, riverside) forest 90. Riparian herbaceous vegetation 91. Swamp forest 92. Swamp forest with palms 93. Riparian thorn forest
94. Mangrove 95. Tall grassland 96. Grassland with woody species 97. Submontane grassland 98. Flooded grassland with palms 99. Grassland with palms
100. Flooded grasslands 101. Flooded grassland and pantanal 102. Salt-marsh community 103. Dunes and restingas

D = Desertic region (driest of the regions with scant vegetation and sectors devoid of plant cover)
N = Glaciers and snow caps

further complicated by the inability to distinguish between savanna and non-savanna grass species and by the swamping of indicator species (e.g., *Bowdichia virgilioides*, *Byrsonima crassifolia*, *Curatella americana*, *Roupala complicata*) by pollen from the surrounding forest. In the Neotropics, expanses of intensively cultivated, frequently burned grassland with scattered trees and shrubs on leached soils in areas with markedly seasonal rainfall (800–2500 mm/yr) include Los Llanos of the Orinoco River, Rupununi of Guyana, coastal savannas of the Guianas, Amazon campos, and Gran Sabana of Venezuela (Sarmiento, 1984).

The Gran Sabana: Above an elevation of ~1400 m, the lowland rain forest and the mid-elevation cloud forest of Venezuela give way to the Gran Sabana covering an area of ~35,000 km^2 south of the Lema Range in the state of Bolívar (Schubert & Huber, 1989). A five-year average MAP at Santa Elena de Uairén at the southeastern edge of the savanna is 1631.4 mm, and the soil is mostly sterile sand derived from the underlying Roraima Group. The understory is composed primarily of grasses or other herbaceous plants. The prominent grasses are *Axonopus pruinosus* and *Trachypogon plumosus*, and the most frequent herbs are *Palicourea rigida* and the sedges *Bulbostylis paradoxa*, *Hypolytrum pulchrum*, and *Scleria cyperina*. Shrubs include *Bonnetia sessilis*, *Clusia* sp., *Euphronia guianensis*, *Gongylolepis benthamiana*, *Ouratea* sp., *Thibaudia nutans*, and *Vantanea minor*, and common tree-shrubs are *Maximiliana* sp. and *Vochysia surinamensis*. The same genera characterize many of the other savannas of northern South America.

Tepuis: These landforms are a particularly notable feature of the Venezuelan landscape (Figs. 1.41, 2.35). They are eroded from rocks of the Roraima Group in the Guayana Highlands and are covered with a mosaic of vegetation types depending primarily on moisture. There are meadows, swamps, gallery forests, dense high forests, open shrubland, and savanna (Granville, 1988; Huber, 1992). Among the prominent species are the fern *Pterozonium spectabile*, the gymnosperm *Podocarpus tepuiensis*, bromeliads such as *Brocchinia hechtioides* and *Lindmania marahuacae*, pitcher plants (e.g., *Heliamphora heterodoxa*), and *Adenanthe bicarpellata*, *Aulonemia* sp., *Bonnetia roraimae*, *Chimantaea mirabilis*, *C. similis*, *Clusia annularis*, *C. multiflora*, *Kunhardtia rhodantha*, *Mallophyton chimantense*, *Marahuacaea schomburgkii*, *Nietneria paniculata*, *Orectanthe sceptrum*, *Schefflera umbellata*, *Stegolepis guianensis*, *S. humilis*, and *Tepuia* sp. Most are related to taxa in the surrounding Gran Sabana and adjacent forests, supplemented by numerous endemics on these isolated mesas.

Figure 3.128. Arid vegetation with columnar Cactaceae (cardonal), northern estado Falcón, Venezuela. From Schnee (1973). Used with permission of the Universidad Central de Venezuela, Maracay, Venezuela.

Figure 3.129. Tropical dry forest with *Pterocarpus podocarpus*, estado Apure, Venezuela. From Ewel et al. (1976). Used with permission of the Ministerio de Agricultura y Cría, Fondo Nacional de Investigaciones Agropecuarias, Caracas, Venezuela.

Table 3.8. Vegetation types of South America according to the classification followed in this text together with approximate equivalent types used on the Vegetation Map of South America (UNESCO, 1980–1981). Numbers refer to those on the UNESCO map; degraded formations + crops are not included.

Desert
D = Desertic region (driest of the regions with scant vegetation and sectors devoid of plant cover).
Shrubland/chaparral–woodland–savanna
4. Grassland with woody species (savanna; within constantly warm regions/extremely moist and very moist formations; 7. within moist formations; 13. within subhumid formations; 38. campos cerrados within regions with a cold season/subhumid formations; 56. within regions with a cold season/nontropical lowland regions; 96. within edaphic formations).
5. Seasonal forest
10. Deciduous forest
11. Xeromorphic forest (within constantly warm regions; 64. within regions with a cold season/nontropical lowland regions)
16. Woodland with succulents (within dry formations; 21. within very dry formations)
17. Drought-deciduous woodland and chaco
18. Thorn forest with succulents
19. Semi-deciduous forest
22. Deciduous woodland
23. Deciduous thicket with succulents
24. Deciduous thicket without succulents
26. Dwarf-shrubland with succulents
35. Semi-deciduous forest and cerradão
36. Thorn forest
39. Dry forest
40. Thorn woodland
41. Submontane thicket and caatinga
42. Deciduous scrub (within tropical submontane regions/dry and very dry formations; 61. within nontropical lowland regions)
55. Subtropical forest and cerrado
60. Sclerophyllous woodland
62. Sclerophyllous thicket
65. Subdesert thorn scrub
66. Evergreen shrubland
67. Semi-deciduous shrubland
Mostly cold, lowland, dry southern forests related to *Araucaria* (80), deciduous (81), subpolar swamp (82) forests:
84. Subpolar deciduous shrubland
85. Deciduous open shrubland
93. Riparian thorn forest
Grassland
14. Grassland (within constantly warm/subhumid regions; 57, 63. [pampa] within nontropical lowland regions)
Edaphic grassland formations:
95. Tall grassland
97. Submontane grassland
98. Flooded grasslands with palms
99. Grassland with palms
100. Flooded grassland
101. Flooded grassland and pantanal
Mangrove
94. Mangrove
Beach/strand/dune
102. Salt-marsh community
103. Dunes and restingas (sandbanks, offshore rocks)
Freshwater herbaceous bog/marsh/swamp
90. Riparian herbaceous vegetation
Aquatic
Lowland Neotropical rain forest
1. Extremely moist forest
2. Very moist forest
8. Evergreen lowland forest (coastal types)
89. Riparian forest (lowland association)
Lower to upper montane broad-leaved forest
28. Extremely moist submontane forest
29. Ombrophilous (very wet) submontane forest
31. Atlantic forest
32. Evergreen submontane forest
44. Montane forest
46. Cloud forest
47. Moist seasonal montane forest
49. Subhumid montane forest
51. Deciduous montane forest
52. Montane deciduous scrub
58. Deciduous forest
Mostly cold, lowland, moist, southern forests:
76. Subpolar forests
77. Broad-leaved forest
78. Valdivian forest (from approximately the city of Valdivia, 40°S, to the Isla de Chiloé, 43°S, Chile)
81. Deciduous forest
82. Subpolar swamp forest
83. Degraded formations + crops
Mostly cold, lowland, dry, southern forests:
84. Subpolar deciduous shrubland (see also shrubland/chaparral–woodland–savanna)
85. Deciduous open shrubland (see 84 above)
89. Riparian forest (upland/slope association)
Swamp forest association:
91. Swamp forest
92. Swamp forest with palms
Coniferous forest (including montane broad-leaved forest with a conspicuous coniferous component)
33. Forest with *Podocarpus* (evergreen submontane forest)
54. Forest with *Araucaria*
80. *Araucaria* forest
86. Tundra
Alpine tundra (páramo)
68. Páramo with woody species
69. Páramo
70. Degraded páramo
71. Moist puna
72. Degraded moist puna
73. Puna
74. Degraded puna
75. Dry puna
87. Bunch-grass community
88. Andine meadow of higher latitudes

A perusal of the geologic maps of northern South America (Chapter 2) shows isolated outcrops of underlying sandstone extending southwest from the Guayana Highlands. Disjunct populations of plants from the tepuis grow on these outcrops, then reappear on similar sterile sandy soils along the eastern slopes of the Andes Mountains near the Peru–Ecuador border (David Neill, pers. comm., 2002). The intervening area in southern Colombia (states of Meta, Guaviare, Caquetá) is covered by eroded sediments from the eastern Andes Mountains, so it is unclear if the sandstones and their plant populations

Figure 3.130. *Mauritia flexuosa* swamp, Manaus, Brazil. From TROPICOS, photograph by Alwyn Gentry. Used with permission of the Missouri Botanical Garden, St. Louis.

once extended across the region. This poses a question, raised by geologic observations, that could be addressed through molecular and population genetics; namely, whether the disjunct distributions evident between the Guayana Highlands and Peru–Ecuador are the result of long-distance dispersal between similar edaphic habitats, or represent a vicariance event when the intervening sterile and older sandstone outcrops were covered by erosion sediments during the late Cenozoic uplift of the Andes Mountains.

Lowland Neotropical rain forest—The rain forests of Venezuela that receive the greatest precipitation (bosque muy húmedo tropical) are found at low elevations, between 50 and 600 m, to the west-southwest at the border with Colombia, and in the far south adjacent to Brazil (No. 6 in Fig. 3.127). Here, the MAP is 3700–5000 mm, but it may reach 8000 mm in some years. The more typical and better-documented maxima are ~5000 mm, and at slightly higher elevations of 1000 m the MAP is 1800–3800 mm. The bosque húmedo tropical occupies extensive areas around the Maracaibo Basin and in the western and southern parts of the country (No. 5 in Fig. 3.127). In Venezuela, prominent tropical rain forest trees include *Carapa*, *Cedrela*, *Ochroma*, *Parkia*, *Scheelea*, and *Warszewiczia*. The formation will be discussed in more detail with reference to its greatest extent in Brazil.

Orinoco River Delta vegetation: This community is of interest because it has been the subject of studies comparing modern spores and pollen in the delta sediments with extant vegetation growing on the delta, in gallery forests, and along the floodplain (Muller, 1959; Hofmann, 2002). Also, the palm *Mauritia* is the prominent component of a specific vegetation type (delta palm swamp, morichales), and it has recognizable pollen that is well-represented in the fossil record. The delta forms where the Orinoco River empties into the Caribbean Sea at the Gulf of Paria south of Trinidad and Tobago. The MAT is 24° C and the MAP is 2800 mm. On the floodplain, the dominant plant over large areas is the aquatic grass *Paspalum repens*, and *Eichhornia crassipes* (water hyacinth) is locally abundant. Fringing the delta there is a mangrove swamp of *Avicennia nitida*, *Laguncularia racemosa*, and *Rhizophora mangle* with *Crenea maritima*. Inland on the delta proper, there is a swamp forest association within the lowland tropical rain forest formation that includes *Bombax*

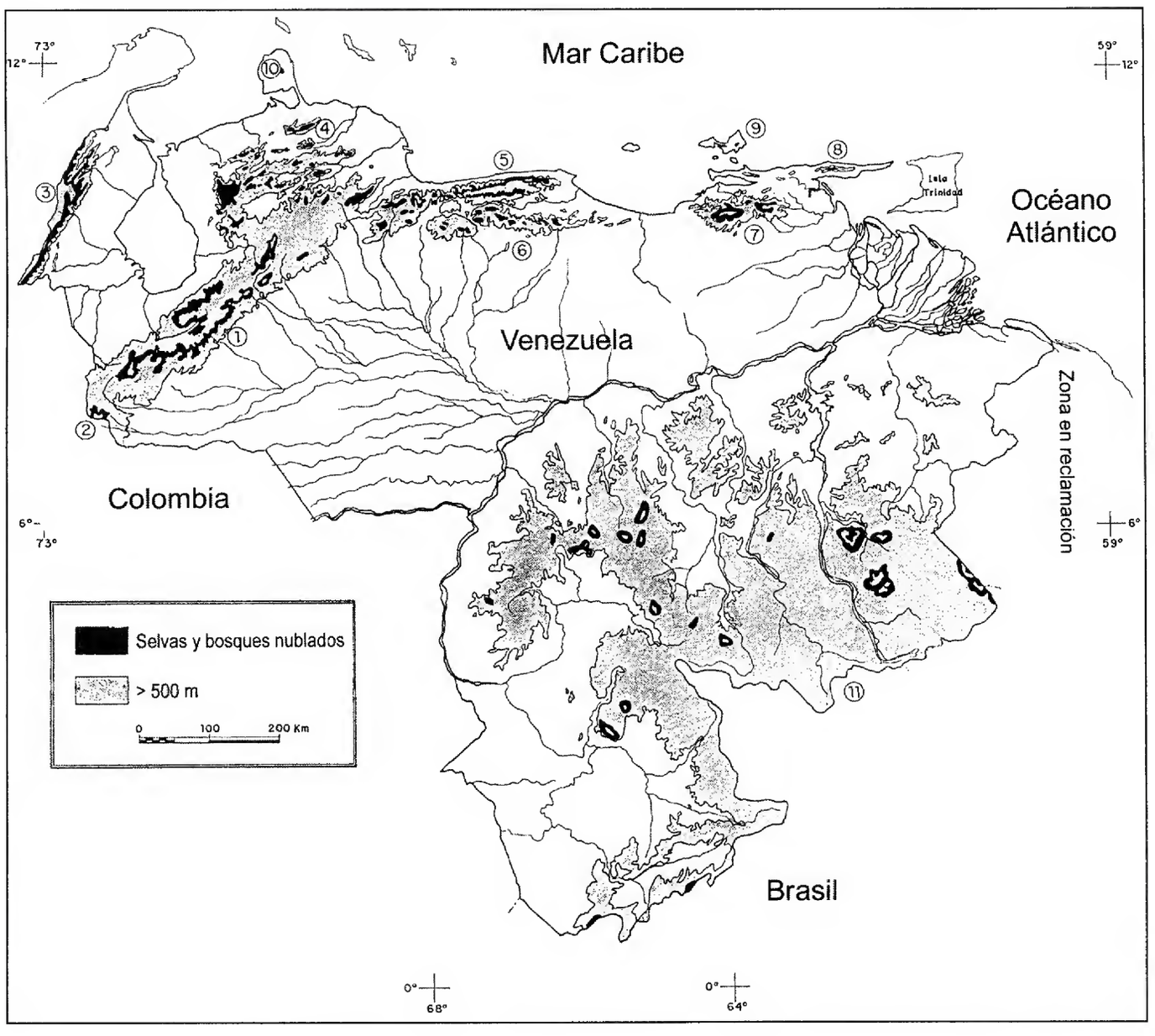


Figure 3.131. Distribution of cloud forest in Venezuela. From Ataroff (2001) in Kappelle and Brown (2001). Used with permission of Editorial INBio, Santo Domingo de Heredia, Costa Rica.

aquaticum, *Cecropia peltata* (open, secondary vegetation), *Ceiba pentandra*, *Cordia alliodora*, *Inga spuria*, *Machaerium lunatum*, *Manicaria saccifera*, *Montrichardia arborescens*, *Ochroma pyramidale*, *Pachira aquatica*, *Pterocarpus officinalis*, *Symphonia globulifera*, and *Terminalia catappa* with locally dominant phases of palms (*Euterpe oleracea*; *Mauritia flexuosa*, Fig. 3.130) and stands of *Erythrina glauca*. A list of Orinoco Delta plants is given by Hoffmann (2002; see also Huber, 1995, pp. 148–149). Palynomorphs recovered from the recent delta sediments include *Mauritia* (6%), *Montrichardia* (3%), *Symphonia* (3%), numerous fern spores (41%; likely reflecting differential preservation of the thick-walled spores), Poaceae (6.5%), and Cyperaceae (4%). Study of the quantitative relationship between these percentages and the representation and arrangement of the modern plants allows a more precise reconstruction of the paleocommunities. For example, Muller (1959) noted that wind transport of pollen in the Orinoco drainage region is secondary to outwash from rain and transport by rivers. None of the shrubs of the dry grasslands and savannas beyond the river watershed (e.g., Los Llanos) were present in the delta assemblages, indicating these formations would be under-represented in plant microfossil floras from this environment. Another observation was that the small (~22 μm) and relatively unornamented pollen of *Rhizophora* is carried farther out to sea than most other types. Therefore, it increases in percentage in delta and continental shelf deposits even though the absolute number of grains decreases (see I: pp. 281–282; Chapter 4).

Lower to upper montane broad-leaved forest—In its wettest phase (~2000–4000 mm) and at the lowest elevations (550–1500 m), this forest is transitional to the lowland Neotropical rain forest; at its driest phase (500–1000 mm) it merges with the shrubland/chaparral–woodland–savanna formation, and at the highest elevations (~3600 m) and in the coldest regions (6°–12° C), it downsizes through ceja into páramo–puna. It is most extensively developed under the intermediate climates of ~18°–24° C MAT, 1500–2500 mm MAP, and at 1000–2500 m elevation. These conditions are found bordering Los Llanos (No. 9 in Fig. 3.127), in the better-drained upland regions within the lowlands (Nos. 9–15 in Fig. 3.127), and at progressively higher elevations along the Cordillera de Mérida–Sierra de Perijá south of the Maracaibo Basin (Nos. 9, 10, 12, 13, 14, 16, 17, 18 in Fig. 3.127). Among the genera characteristic of this forest in Venezuela are numerous tree ferns of the family Cyatheaceae, *Podocarpus*, *Bocconia*, *Bonnetia*, *Bravaisia*, *Brocchinia*, *Brunellia*, *Calophyllum*, *Chrysophyllum*, *Clusia*, *Euterpe*, *Ficus*, *Gyranthera*, *Heliamphora*, *Heliconia*, *Heliocarpus*, *Lecythis*, *Lippia*, *Lonchocarpus*, *Miconia*, *Ocotea*, *Oreopanax*, *Palicourea*, *Protium*, *Psychotria*, *Pterocarpus*, *Saurauia*, *Sloanea*, *Stegolepis*, *Tabebuia*, *Tibouchina*, *Tyleria*, and *Weinmannia*. In addition, there are several genera familiar from the montane broad-leaved forest in northern Latin America such as *Alnus*, *Ilex*, *Myrica*, *Prunus*, *Salix*, *Trema*, and *Vaccinium*. Lichens, epiphytic ferns, and bromeliads (e.g., *Tillandsia*) give a cloud forest aspect to the bosque muy húmedo montano beginning around 2500 m elevation. Ataroff (2001, table 5) lists other representative species of the

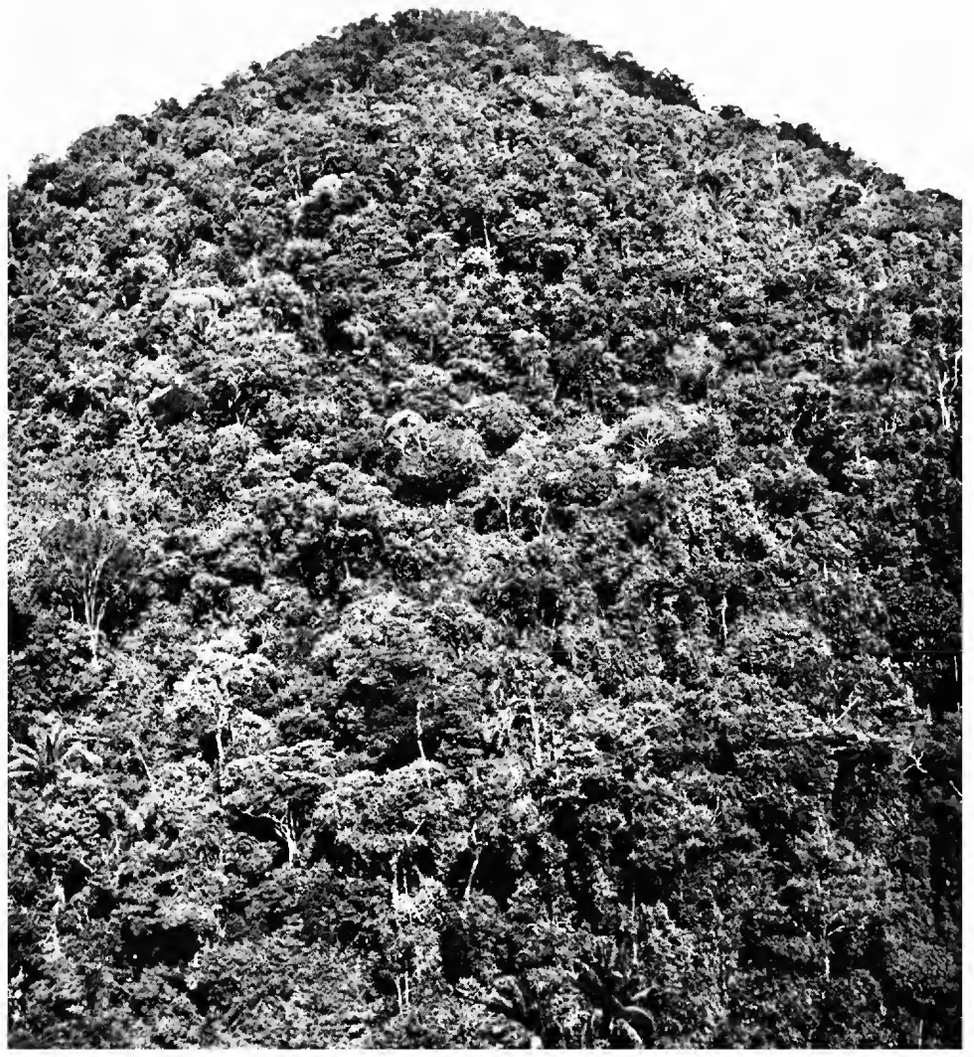


Figure 3.132. Premontane wet forest, estado Bolívar, Venezuela. From Ewel et al. (1976). Used with permission of the Ministerio de Agricultura y Cría, Fondo Nacional de Investigaciones Agropecuarias, Caracas.

formation (see also Appendix 1.17; Figs. 3.131, 3.132).

Alpine tundra (páramo)—This plant formation is found at the highest elevations in the Sierra de Perijá, generally above 3600 m, where the MAP is from 3° to –6° C. The most conspicuous plant is *Espeletia schultzii*, growing with grasses (*Aciachne pulvinata*), composites (*Senecio*), and other herbaceous flowering plants (*Hypericum*; Appendix 1.17). The páramo will be discussed further in the section on Colombia, which includes information on the modern community and its late Cenozoic history.

As floras, checklists, and monographs are completed for the vegetation of Latin America (Appendix 1) and more fossil floras are described (Appendix 2), a relationship becomes apparent between certain lineages and plant formations and the time of their appearance. For the moment, the analyses are limited by the strengths and limitations of the various paleobotanical methods, including the geographic and stratigraphic unevenness of the data and the quality of identifications, especially in the older literature. Eventually, the inventory of fossil plants will have to be better organized, databased, and assessed for its geologic, paleoecological, and phylogenetic plausibility. Nevertheless, the data for Venezuela can serve as an example of the use of the tables and appendices in conjunction with paleobotanical information. If a tabulation is made of genera that are (1) prominent in the driest habitats of Venezuela (or that range into those habitats from moister areas; Appendix 1.17; Ewel et al., 1976; Steyermark et al., 1995 et seq.), and (2) also

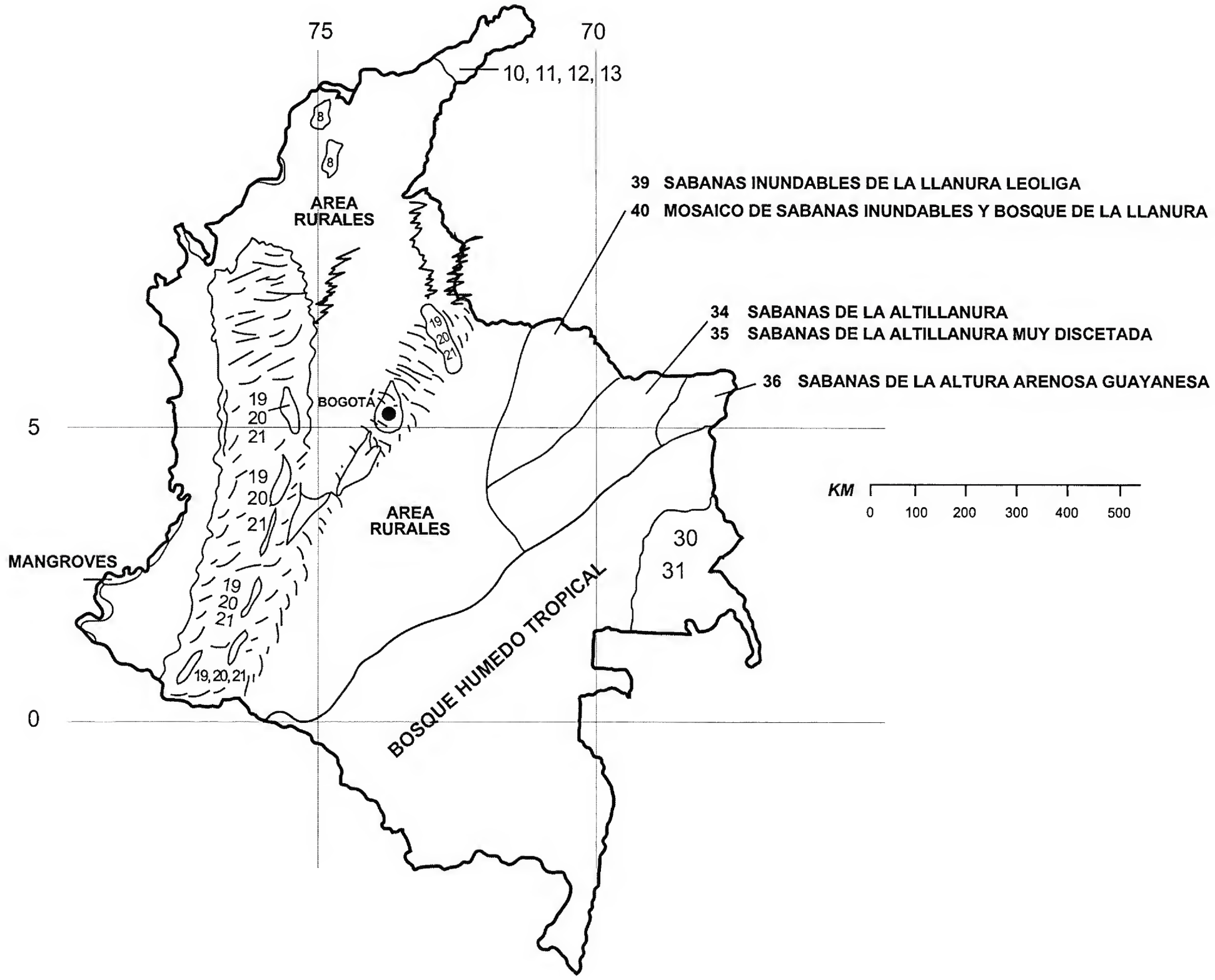


Figure 3.133. General index map of the principal plant formations of Colombia (based on Etter, 1998). Etter's vegetation types 1–7 and 9 (not included on Fig. 3.133) are scattered through the western half of the country and are described as "areas rurales" with only 20%–50% of the natural vegetation remaining (mostly various types of savanna). 8—Bosque seco tropical; 10, 11, 12, 13—Desert (desierto tropical); 19, 20, 21—Páramos húmedos, páramos secos, superpáramo; 30, 31—caatingas; 34—Sabanas de altillanura; 35—Sabanas de altillanura muy disectada; 36—Sabanas de la altura arenosa Guyanesa; 39—Sabanas inundables de la llanura; 40—Mosaíco de sabanas inundables y bosque de la llanura.

have a fossil record in South America, the following appear on both lists: *Acnistus*, *Byrsonima*, *Castela*, *Cereus*, *Chlorophora*, *Croton*, *Curatella*, *Didymopanax*, *Dodonaea*, *Guaiacum*, *Guarea*, *Hyptis*, *Opuntia*, *Phyllanthus*, *Pouteria*, *Prosopis*, and *Spondias*. A similar compilation for the páramo includes *Jamesonia*, *Arenaria*, *Calceolaria*, *Draba*, *Fuchsia*, *Gaultheria*, *Gentiana*, *Hypericum*, *Lupinus*, *Montia*, *Plantago*, and *Rhizocephalum*. A feature of both is that the fossils are all known only from the latest Pliocene–Quaternary, consistent with the assumed recent geologic appearance of these habitats and communities in South America and elsewhere. If elements for plant formations such as aquatic, mangrove, lowland Neotropical rain forest, and lower to upper montane broad-leaved forest are tabulated, they are found to extend much further back in time. A host of refinements will be necessary before these sequences and relationships are better established, but they are evident enough from study of the past and present vegetation of Venezuela to demonstrate the potential value of the two tabulations for dating the relative appearance of ecosystems.

Colombia

There is a radar survey of Colombian vegetation (PRORADAM, Proyecto Radargrametrico del Amazonas, 1979), a life zone map (Espinal & Montenegro, 1963), a description of the vegetation regions (Rangel-Ch. et al., 1997; Rangel-Ch., 2000), a flora of the Parque Nacional Natural Amacayacu (Rudas Lleras & Prieto Cruz, 2005), and an ecosystem map of Colombia (Etter, 1998). The latter shows the western two-thirds of the country as highly disturbed "areas rurales" (Fig. 3.133). In this region, 50%–80% of the natural vegetation has been

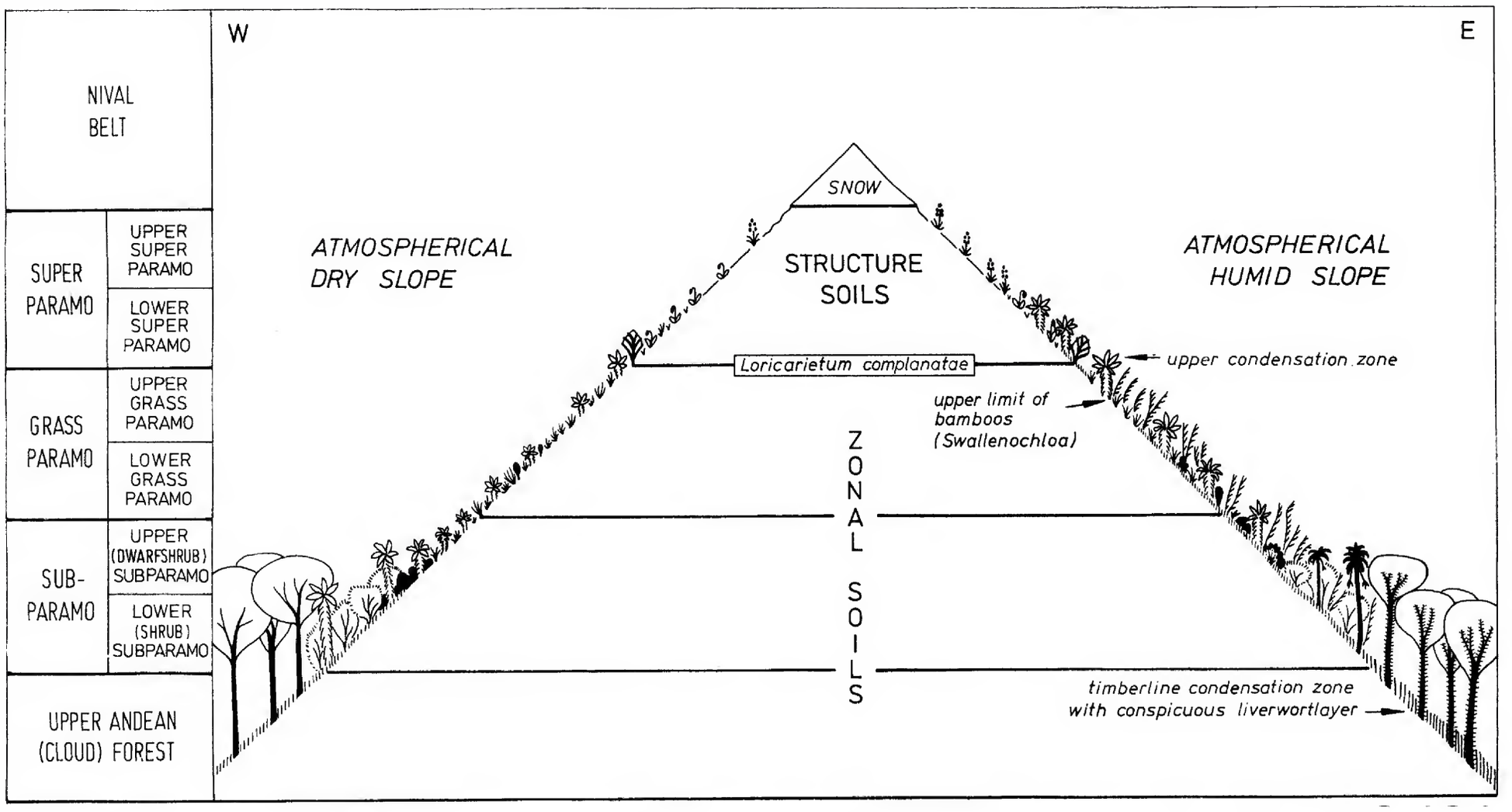


Figure 3.134. Zonation of páramo vegetation, Cordillera Oriental, Colombia. From van der Hammen and Cleef (1986) in Vuilleumier and Monasterio (1986). Used with permission of Oxford University Press, Oxford, U.K.

destroyed, and it has been replaced by a much-expanded savanna and associated shrubby communities of *Curatella americana*, *Byrsonima crassifolia*, *Bowdichia virgilioides*, *Casearia sylvestris*, *Palicourea rigida*, and *Roupala complicata* (Cavelier et al., 1998). There are also remnants of desert and desertified vegetation on the Colombian part of the Guajira Peninsula mentioned earlier with reference to Venezuela. The woodland/chaparral–shrubland–savanna (bosque seco tropical, caatingas, sabana) makes up a large part of the areas rurales, and it extends eastward from Colombia into Venezuela as part of Los Llanos. There are mangroves scattered along the Pacific coast and around the Atrato lowlands adjacent to Panama.

The Colombian Chocó—A distinctive region of the country known as the Colombian Chocó consists principally of the lowlands along the Pacific coast from Buenaventura–Tumaco, northward through Panama, to the Costa Rica–Nicaragua border (Mora et al., 2006; Fig. 1.34) and includes the San Juan and Atrato river valleys. It has been called "the wettest region in the world" with Tutunendo "perhaps the rainiest place in the world, 11,770 mm" (Gentry, 1986; see footnote 2, Chapter 1), and later as among the wettest regions in the world (Faber-Langendoen & Gentry, 1991). The MAP at other sites within the Chocó is 7470 mm at Pulpapel Station (elevation 100 m), 8558 mm at Quibdó, and 9000–10,000 mm at Tutunendo (elevation 90 m). MAT is 27.3° C and relative humidity is >85%. The Estación Biológica El Amargal is located on the Pacific coast, and the Río Palenque Science Center is near the drier southern limits of the Chocó in adjacent Ecuador (MAP of 2980 mm; Dodson & Gentry, 1978).

The vegetation is a very dense lowland Neotropical rain forest with canopy trees 30–40 m tall covered with epiphytic fungi, algae, lichens, mosses, ferns, bromeliads, orchids, and hemiepiphytic vines. In the Holdridge system, it is a tropical wet (bosque muy húmedo tropical) to tropical pluvial (bosque pluvial tropical) forest. On the slopes at 500–600 m there is cloud forest–like vegetation, but because of the high precipitation it shares many elements with the rain forest.

In addition to the rainfall, there are references to record species diversity. "The lowland pluvial forests of the Colombian Chocó are the most species-rich plant communities in the world" (Gentry, 1986), although this has been scaled back somewhat in recognition that such estimates depend on the method used to measure diversity. Whatever the ranking, these forests are very wet and impressively rich with an average of 262 species ≥2.5 cm (1 in) in dbh in only 0.1 ha, and 250 tree species ≥10 cm/ha. Representative species are listed in Appendix 1.18.

An observation of interest for paleoenvironmental reconstructions based on leaf physiognomy is further documentation and some quantification of the association of large leaf size with high precipitation (I: pp. 124–128). The Colombian Chocó, with areas of annual rainfall of ~11,000 mm, nearly perpetual cloud cover, high humidity, and shaded habitats, may also have "world records for leaf size" (Gentry, 1986, p. 83). Those with putatively "the largest leaves known in the entire world for their families" include *Schlegelia dressleri* (Bignoniaceae), *Psittacanthus* (Loranthaceae; leaves 50–100 cm long), *Licania gentryi* (Chrysobalanaceae), *Iryanthera megistophylla* (Myristicaceae), and *Ilex* (Aquifoliaceae; 15–25 × ca. 10 cm, or up to five times the length of holly leaves in the north).

Figure 3.135. View of the páramo de Piedras Blancas (4200 m) with *Espeletia*. Photograph by Mario Fariñas, used with permission of Mario R. Fariñas.

The southeastern one-third of Colombia is potentially lowland Neotropical rain forest (bosque húmedo tropical; Duivenvoorden & Lips, 1995), riverine vegetation, and lowland, wet phases of the lower to upper montane broad-leaved forest (Cavelier et al., 2001). Other altitudinally zoned phases of the latter community would also extend up the slopes of the Cordillera Occidental, Cordillera Oriental, and the Cordillera (Sierra) Perijá, but this is one of the most intensely farmed and heavily lumbered regions of Colombia.

Figure 3.136. *Espeletia hartwegiana* and *Calamagrostis coarctata* (>3700 m), Laguna del Ruiz, Cordillera Central, Colombia. From Troll (1968). UNESCO (In Kommission bei Ferd. Dümmlers Verlag, Bonn, Germany).

Elsewhere in Colombia the subandean forest (~1200–2300 m) and Andean forest (~2300–3500 m) are better preserved and give an indication of their geographic affinities. In the Andean forest of the Cordillera Oriental, among 130 woody genera tabulated, 82% were tropical, 10% holarctic, 6% austral–antarctic, and 2% undetermined (van der Hammen & Cleef, 1986). In the tropical group, 8% were tropical amphi-Pacific (that is, they occur in the Neotropics and in southeastern Asia), including *Bocconia*, *Clethra*, *Guettarda*, *Hedyosmum*, *Laplacea*, *Meliosma*, *Murraya*, *Persea*, *Saurauia*, *Sloanea*, *Styrax*, *Symplocos*, *Talauma*, *Toxicodendron*, and *Turpinia*. This relationship is of interest because *Trigonobalanus* (Fagaceae) was discovered here in the Cueva de los Guácharos National Park, Upper Magdalena Valley (Lozano-C. et al., 1979; Hernandez-C. et al., 1980; van der Hammen, 1983). Until that time, the genus was known only from two species, *T. verticillata* in the Celebes, Borneo, and Malaya, and *T. doichangensis* in Thailand (Nixon & Crepet, 1989). The fruits are not especially adapted to long-distance dispersal, and *Trigonobalanus* has no fossil record in Latin America, so its migration route is unknown. The most direct overland pathway would be from Southeast Asia through Beringia and across the isthmian land bridge, suggesting that like *Alnus* and *Quercus*, its entry into the Andean forests was recent. This route is supported by reports of *Trigonobalanus* fossils from the Paleocene–Eocene of Tennessee (Crepet & Nixon, 1989a) and from the Oligocene of Texas (Crepet & Nixon, 1989b).

Páramo—

> "Biologists say climate change may already be affecting high-mountain ecosystems around the world, where plants and animals adapted to cold, barren conditions now face higher temperatures and a surge of predators and competitors." (Krajick, 2004)

The páramo of Colombia has been the subject of several eco-floristic and paleoecological studies (Cleef, 1979, 1981; van der Hammen & Cleef, 1986), and part of broader regional studies (Cuatrecasas, 1957; Monasterio, 1980; Balslev & Luteyn, 1992; Cleef & Chaverri, 1992; Luteyn, 1992, 1999; Luteyn et al., 1992). Páramo is a high-altitude ecosystem extensively developed in the Andes Mountains of northern South America (Colombia; Venezuela; Ecuador, Lauer et al., 2001). It occurs above the montane forest (3000–3500 m) and below the permanent snow line (4800–5000 m; Luteyn, 1992; Fig. 3.134), and it covers ~2% of the Northern Andes Mountains. Small outliers occur in Panama, Costa Rica, and Mexico, and in Peru southward. Diurnal temperatures range from –3° C to 12° C, radiation levels are high, and MAP varies from 500 mm to more than 3000 mm. In the drier páramo, bunchgrasses (*Calamagrostis* [*Swallenochloa*] *effusa*, *Festuca*) are dominant, and in the humid páramo, the bamboo grass *Chusquea tessellata* is common. Giant rosette plants of *Espeletia* (Asteraceae; Figs. 3.135, 3.136) and *Puya* (Bromeliaceae; Fig. 3.137) are frequent in the north. The mostly drier communities in Argentina, southern Peru, and Bolivia are called puna, and in Peru they are also known as jalca.

The páramo includes an estimated 3000–4000 species. The largest families are the Asteraceae (84–100 genera), Poaceae (53 genera), and, surprising to many temperate-trained biologists, the Orchidaceae (22 genera). In this extreme environment, about 60% of the species are endemic. Lichens are prominent, with 264 species presently known, which represent about one-half of the estimated lichen flora of Colombia. Most also are found at lower elevations, suggesting recent arrival by migration rather than by abrupt long-distance transport, or by a long period of in situ evolution (Sipman, 1992). A selected list of plant species in the páramo of the Cordillera Oriental in Colombia is given in Appendix 1.19. Shrubs of *Acaena* (Rosaceae) and the dwarf tree *Polylepis* (Rosaceae) are noteworthy because their similar pollen is well preserved in Quaternary deposits in the Andes Mountains, and it is useful in detecting altitudinal shifts in tree line with changes in climate. Also, the most recently evolved species of *Polylepis* occur at the highest elevations (Simpson, 1979), consistent with the relation between the developing páramo habitats and the evolution of clades adapted to the harsh conditions.

This relationship and its recent origin are further shown by the diversification of *Lupinus* in the Northern Andes after uplift to their highest elevations in the late Pliocene and Quaternary. The age of a clade, including 81 endemic species, is estimated at 1.18–1.76 Ma for a speciation rate of 2.49–3.72 species/Ma, "providing the most spectacular example of explosive plant species diversification documented to date" (Hughes & Eastwood, 2006).

A major portion of the páramo has been highly modified through fire, grazing, cultivation, and lumbering. In contrast to most mountainous countries, where cities are typically located in the lowlands and at mid-elevations along mountain slopes, in the Northern Andes most of the population lives in the highlands—50% in Ecuador, 70% in Venezuela, and 75% in

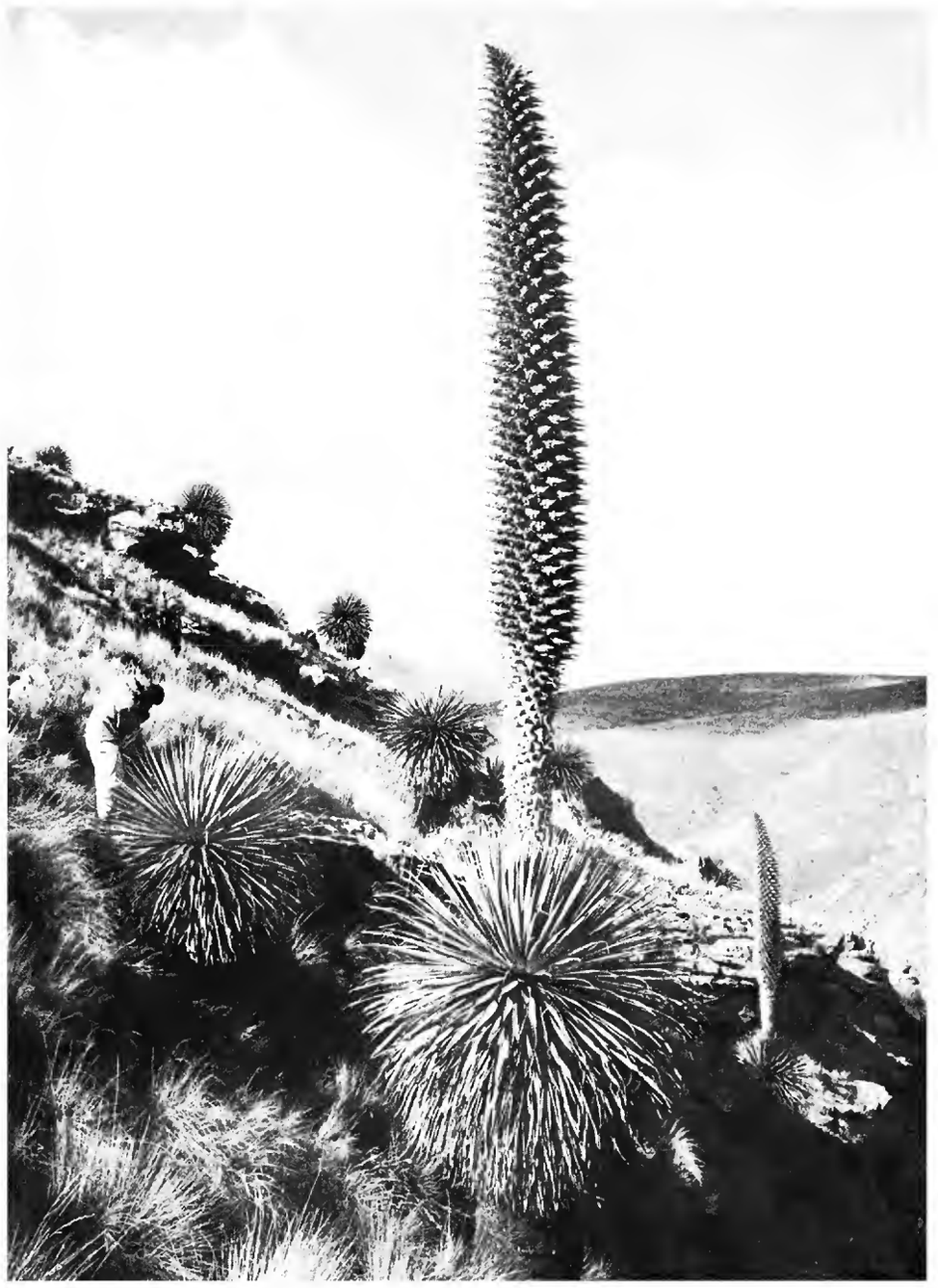


Figure 3.137. *Puya raimondii*, Peruvian Puna. From Weber (1969) in Fittkau et al. (1969). Used with permission of Dr. W. Junk Publishers, The Hague.

Colombia (Luteyn, 1992). Disturbance of high-altitude ecosystems dates back to ~900 A.D. in northern Peru (Schjellerup, 1992), and after the mid-1500s, human impact was widespread throughout the Northern Andes. In Ecuador, forests occur to 4000 m elevation, so grass páramo below that is likely a result of human disturbance, while the origin of other types of páramo involved late Cenozoic climatic changes and evolutionary-speciation responses to the cooling of that period. It has even been suggested that the high-altitude grass páramo may be entirely of human origin through fire (Laegaard, 1992; but see Wille et al., 2002).

The preservation of páramo is important because it serves as the principal water catchment, filtration, and regulation system for population centers like Bogotá with its 7 million people. The 58,000-ha Chingaza National Park near Bogotá has the highest MAP recorded for any páramo (3000 mm). Other sites under at least nominal protection are Chirripó (Costa Rica); Sierra Nevada de Mérida and Piedras Blancas (Venezuela); Sierra Nevada de Santa Marta, Los Nevados, and Puracé (Colombia); and Cotopaxi, Sangay, and Podocarpus (Ecuador). An understanding of the páramo as a natural ecosystem, or as a complex of ecosystems depending in part on human activity,

is essential for developing sustainable management practices, and part of that information is preserved in the plant fossil assemblages of the high Andes Mountains.

Ecuador

> "Humboldt was one of those wonders of the world, like Aristotle, like Julius Caesar, like the admirable Crichton, who appear from time to time as if to show us the possibilities of the human mind, the force and range of the faculties… ." (Ralph Waldo Emerson, quoted from de Terra, 1955)

Study of the vegetation of Ecuador had illustrious beginnings with the observation of Alexander von Humboldt (1807) that the structure and composition of tropical plant communities change with altitude, and that the changes are comparable to the change with latitude. This established a causal relationship between climate and plant and animal distributions that was fundamental to the developing fields of biogeography and ecology.

The vegetation of Ecuador is comparatively well known through the *Catalogue of the Vascular Plants of Ecuador* (Jørgensen & León-Yánes, 1999), the ongoing *Flora of Ecuador* project (Harling & Sparre, 1973 et seq.), Botánica Sistemática Ecuadoriana (Freire-Fierro, 2004), review articles (Grubb et al., 1963; Harling, 1979 [includes a vegetation map]; Balslev, 1988), checklists (Jørgensen & Ulloa Ulloa, 1994; Renner et al., 1990), a flora of trees and shrubs (Ulloa Ulloa & Jørgensen, 1993; floodplains, Balslev et al., 1987; páramo, Ulloa Ulloa et al., 2004), and local floras (Dodson & Gentry, 1978; Dodson et al., 1986). There is also a Holdridge life zone map (Cañadas Cruz, 1983), a map of the actual vegetation (Sierra, 1999a) with accompanying text (Sierra, 1999b), and one of the potential natural vegetation (Sierra et al., 1999). The vascular flora is estimated at ~20,000 species, about the same as North America north of Mexico, which is six times the size. From 1973 to 1998, 4000 new plant species were described from Ecuador for a rate of one new species every two days. The region between the Eastern Cordillera of the Andes Mountains and the Amazon lowlands in Ecuador is called the Cóndor, and it has an especially high level of plant diversity. In an area of ~11,000 km^2, there are an estimated 4000 species. Endemic plants in Ecuador number ~4500, and within the mid-elevation communities (900–3000 m) endemism is 39% (Balslev, 1988; see also Kessler, 2002). An index map of the vegetation is shown in Fig. 3.138, and the plant formations with representative species are given in Appendix 1.20.

Considerable effort has been made to preserve the natural biota of Ecuador, and with some notable successes. There is the Sumaco Napo–Galeras National Park that is now a UNESCO Biosphere Reserve on the eastern slopes of the Andes Mountains; the Mache-Chindul Ecological Reserve in the Pacific coastal range; the Llanganates National Park and Antisana Ecological Reserve in the high Andes Mountains; and El Cajas National Park in the páramo. There is a 5000-acre Jatun Sacha Biological Station with its Amazon Plant Conservation Center in the Amazon lowlands, and the new Quito Botanical Garden. Even so, ~300,000 acres of forest and an estimated 160 species are lost each year to lumbering. Although few studies on vegetation history are in progress in Ecuador at present (see Chapter 8, Refugia), the detailed information being compiled on the modern ecosystems is valuable for interpreting paleoecological results from elsewhere in the Neotropics.

The driest areas of Ecuador are on the coast of Guayas (Santa Elena Peninsula), under the influence of the cold Humboldt Current, where the MAP is ~300 mm and there is a nine-month dry season. The prominent plants are columnar cacti (*Armatocereus*) and shrubs of *Bursera*, *Capparis*, *Loxopterygium*, *Maytenus*, and *Vallesia*. In areas where MAP increases to ~1500 mm and the dry season is reduced to about seven months, as in parts of lowland coastal Ecuador, the vegetation is a shrubland/chaparral–woodland–savanna that is mostly disturbed and has greatly expanded through human activity. Among the prominent shrubs are *Cavanillesia*, *Ceiba*, *Eriotheca*, *Machaerium*, *Pradosia*, *Pseudobombax*, *Pseudosamanea*, and *Samanea* (Appendix 1.20). The transition to the dry phase of the lower to upper montane broad-leaved forest occurs where MAP is between 1500 and 2500 mm and the dry season is about three months long. Remnants are found in the dry interandean valleys usually between 200 and 3000 m elevation, on the steep slopes of ravines (quebrada vegetation), and in coastal west-central Ecuador. The principal genera are *Ephedra americana* (Ickert-Bond, 2002), *Acacia*, *Agave*, *Attalea*, *Bejaria*, *Brosimum alicastrum*, *Caesalpinia*, *Cantua*, *Castilla*, *Centrolobium*, *Cercidium*, *Croton*, *Dodonaea*, *Erythrina*, *Gallesia*, *Hypericum*, *Lomatia*, *Opuntia*, *Oreocallis*, *Phytelephas*, *Poulsenia*, *Prosopis*, *Pseudobombax*, and *Tillandsia*. Some are spiny, such as *Barnadesia*, *Duranta*, *Hesperomeles*, and *Mimosa*, and these form local chaparral-like phases. Streams through the dry landscape support *Salix humboldtiana* (willow) and *Schinus molle* (pepper tree).

Throughout the long period of human occupation in Latin America, economically important plants such as palms (e.g., *Attalea* and *Phytelephas*) are often left standing, and it is now unclear whether existing upland palm stands or palm savannas in Ecuador, or indeed anywhere in the Neotropics, are natural ecosystems (in contrast to vereda; see Brazil). As noted for Mexico, there is no convincing evidence for these upland phases in the fossil record of South America without evidence of human activity.

The most extensive mangroves are along the coast of Esmeraldas Province, and they include the widespread *Avicennia*, *Conocarpus*, *Laguncularia*, and *Rhizophora*, in addition to the western Central American–northern South American *Pelliceria*. Mangroves are important as filters of silt and as barriers to erosion, but the habitats can also be converted into brackish-water ponds for cultivating shrimp. There has been rapid, unplanned, and unmanaged clearing of mangroves for this purpose, and undoubtedly the ecological consequences will become evident with time.

Inland from the mangroves and semi-deciduous forest in the

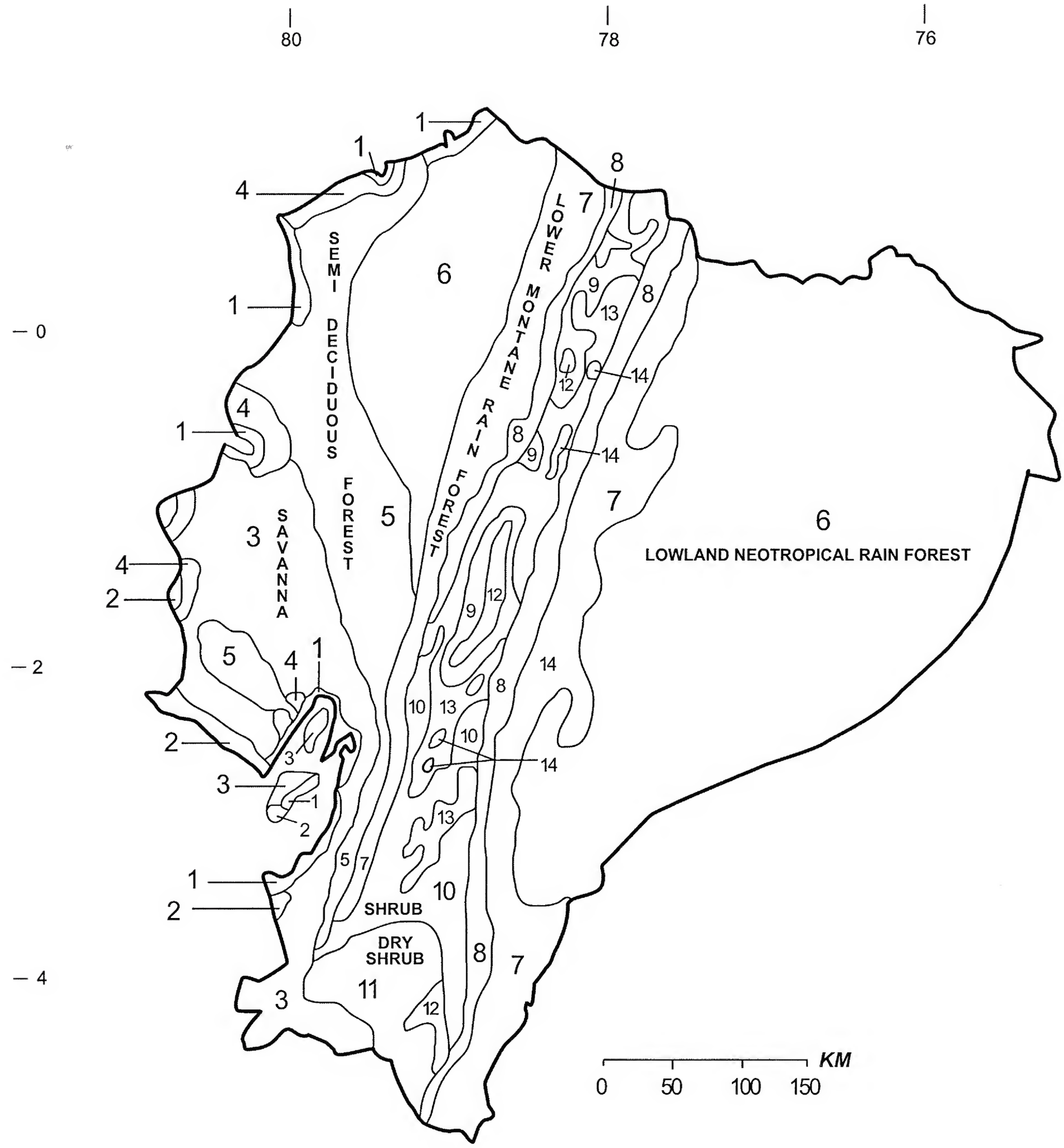


Figure 3.138. General index map of the principal plant formations of Ecuador (based on Harling, 1979; see also Jørgensen & León-Yánez, 1999). 1 = mangrove, 2 = coastal desert and semi-desert, 3 = savanna, 4 = deciduous forest, 5 = semi-deciduous forest, 6 = lowland rain forest, 7 = lower montane rain forest, 8 = cloud forest, 9 = grassland/savanna (disturbed; formerly low woods, ceja [northern Ecuador]), 10 = shrub vegetation (southern Ecuador), 11 = dry scrub (southernmost Ecuador), 12 = interandean desert and semi-desert, 13 = grass páramo, 14 = shrub and cushion páramo with desert páramo at scattered highest elevations.

western Esmeraldas Province, there is a lowland Neotropical rain forest. This plant formation also covers the eastern two-thirds of the country (Fig. 3.138). It has all the characteristics typical of the rain forest, including unparalleled diversity with 110–300 tree species/ha. Ecuador is one of the "megadiversity" countries of South America, and along with Columbia, Peru, and Brazil, covering only 0.2% of the Earth's surface, these rain forests contain 5% of the Earth's vascular plants. The canopy trees reach 30 m in height. Other typical rain forest features are the warm temperatures (~25° C), high rainfall (MAP >3000 mm), little seasonality, buttressing, many leaves with drip-tips, and numerous lianas and epiphytes. Plants characteristic of the rain forest in Ecuador are listed in Appendix 1.20, and an analysis of the pteridophytes and Melastomataceae along edaphic gradients in the Yasuní National Park is given by Tuomisto et al. (2002).

On the eastern and western slopes of the Andes Mountains, between about 700 and 3600 m, there is a lower to upper montane broad-leaved forest formation that includes transition associations to the wetter lowland Neotropical rain forest, the drier shrubland/chaparral–savanna, and the high-altitude páramo or puna. At mid-elevations (2500–3600 m), there is a cloud forest (Sarmiento, 2001), or upper montane rain forest in Webster's (1995) terminology, and at the highest elevations, there is an elfin forest or ceja. The cloud forest has a combination of genera that produce sufficiently distinctive pollen that can be recognized in fossil assemblages (*Alnus*, *Cedrella*, *Clethra*, *Clusia*, *Ilex*, cf. *Oreopanax*, *Symplocos*, *Viburnum*, *Weinmannia*). This information has been used in reconstructing the uplift history of the Central Andes Mountains from paleobotanical evidence (Chapter 7).

There are various types of páramo in Ecuador including grass páramo (3400–4000+ m), shrub and cushion páramo (4000–4500 m), and desert páramo (4500–4900 m). These have been described previously for Colombia, and they are similar in composition. However, the extensive paleoecological studies made on the páramo of Colombia have not been made in Ecuador, and that affords a worthwhile research opportunity.

Peru

One of the early plant-collecting expeditions into South America was by Hipólito Ruiz López and José Pavón between 1777 and 1788 to Peru under the patronage of King Charles III of Spain. The significance of the Ruiz and Pavón collections, and the monumental efforts and often frustrating experiences are chronicled in Steele's (1964) book, *Flowers for the King*. Recall that this was 30 years before the visit of Alexander von Humboldt to Ecuador in 1807, and 55 years before Charles Darwin landed in South America in 1832.

Publication of the *Flora of Peru* began in 1936 (Macbride, 1936 et seq.). While that project progresses, a catalog of the angiosperms and gymnosperms has been published by Brako and Zarucchi (1993), and there is a summary of the vegetation and life zones of Peru (Tosi, 1960; ONERN, 1976), a separate treatment of the ferns and allied groups (Tryon & Stolze, 1989 et seq.), a discussion of the economically important plants (Mostacero León et al., 2002), a flora of the Reservas Biologicas de Iquitos in northern Peru (Vásquez Martínez, 1997), a guide to the trees (Pennington et al., 2004), and a study of floristic diversity in northern Peru (Sagástegui Alva et al., 1999 et seq.).

The flora consists of ~17,143 species of seed plants as listed in Brako and Zarucchi (1993), and the plant communities are generally distributed according to the physiographic provinces of Peru—coastal desert, Andes Mountains, montaña or eastern foothills, and the Amazon lowlands (Chapter 1). The Cordillera Oriental supports a high-altitude puna vegetation with forested communities on the adjacent eastern slopes. On the high grassy Junín plains (>4000 m) there is *Calamagrostis*, *Festuca*, and *Stipa*, and wet areas with Cyperaceae (sedge mats) and *Azorella*, *Distichia*, and *Plantago rigida* (cushion plants). The shrubby puna includes *Baccharis*, *Buddleja*, *Escallonia*, *Gynoxys*, *Miconia*, and *Polylepis* with scattered *Hedyosmum* and *Weinmannia*. Lower in the cloud forest zone, there are more closed communities of *Podocarpus* (*Prumnopitys*), *Escallonia*, *Hedyosmum*, *Symplocos*, and *Weinmannia*, and in the montane forest *Alcalypha*, *Alchornea*, *Alnus*, *Bocconia*, and *Juglans*. Dry valleys cut across the Andes Mountains, facilitating east-west migration and forming

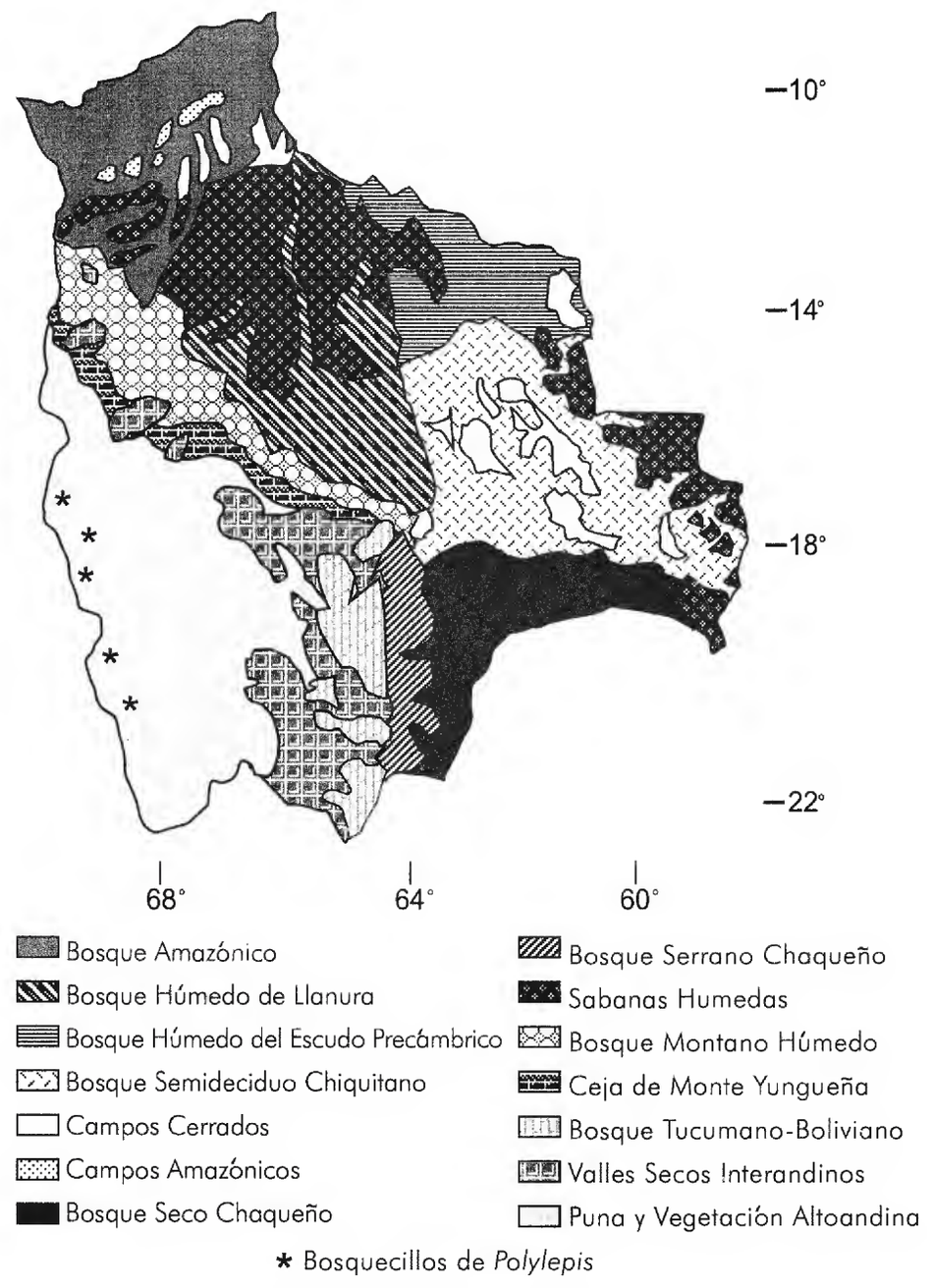


Figure 3.139. Vegetation map of Bolivia. Based on Killeen et al. (1993).

barriers to north-south migration, and the largest is the Huancabamba Valley in northern Peru.

Diversity increases toward the lowlands. Gentry (1986, p. 75) notes that "the most diverse Neotropical samples from outside the chocó region are from the wet aseasonal forests near Iquitos in Amazonian Perú (249 species)" (≥2.5 cm in diameter in 0.1 ha). About 31% of the plant species are endemic to Peru, and endemism is especially high in the mid-elevation habitats (van der Werff & Consiglio, 2004). Remnants of the Peruvian rain forest are preserved in the Manu National Park's Cocha Cashu Field Station (Gentry & Terborgh, 1990; Terborgh, 1990) and in the UNESCO Biosphere Reserves of Huascarán, Noroeste, and Manú (Karez et al., 1998). Other vegetation types are under study in the Los Amigos Conservation area and at the research station at Madre de Dios (BRIT, Botanical Research Institute of Texas; ACA, Amazon Conservation Association).

There is limited paleobotanical information available for Peru (Chapter 7).

Bolivia

The present-day vegetation of Bolivia is known through the studies of Killeen et al. (1993) on the trees and shrubs; Mihotek (1996) on natural communities and biodiversity; Nee (2004) on the flora of the Parque Nacional Amboró in the vicinity of Santa Cruz, central Bolivia; the extensive summary by Navarro and Maldonado (2002) on the ecological geography of the vegetation and aquatic environments; and other publications on limnological aspects of Lake Titicaca (Dejoux & Iltis, 1992), the dry forests (Parker, 1993), and aquatic ecosystems (Chernoff & Willink, 1999). The impressive biodiversity is evident from the ~8000 species in the 30,000-km^2 Madidi National Park in the northwestern part of the country (Jørgensen et al., 2005) and the new 50,000-ha Estación Biológica El Refugio Huanchaca of the Weeden Foundation (http://www.weedenfdn.org) adjacent to the Noel Kempff Mercado National Park. The importance of these preserves is shown by the recent discovery of a new monkey at Madidi: "Finding a new species is always a big deal…and finding a new species of monkey is a huge deal" (Wallace, 2005). A checklist of the plants of Bolivia (Jørgensen, pers. comm., 2003) is being prepared as part of a coordinated project between the Missouri Botanical Garden, the New York Botanical Garden, the National Herbarium of Bolivia in La Paz, the National Forestry Herbarium in Cochabamba, and the Herbarium del Oriente Boliviano in Santa Cruz.

A vegetation map of Bolivia is shown in Fig. 3.139 based on Killeen et al. (1993). The 14 communities outlined on that map, with representative species, are arranged according to the plant formations recognized in the present text in Appendix 1.21. The Chiquitano dry forest is the largest remaining track of seasonally dry forest in the Neotropics. Of interest for vegetational history and paleoenvironmental studies is the lower to upper montane broad-leaved forest formation (Kessler & Beck, 2001; Fig. 3.140). It consists of a number of tropical

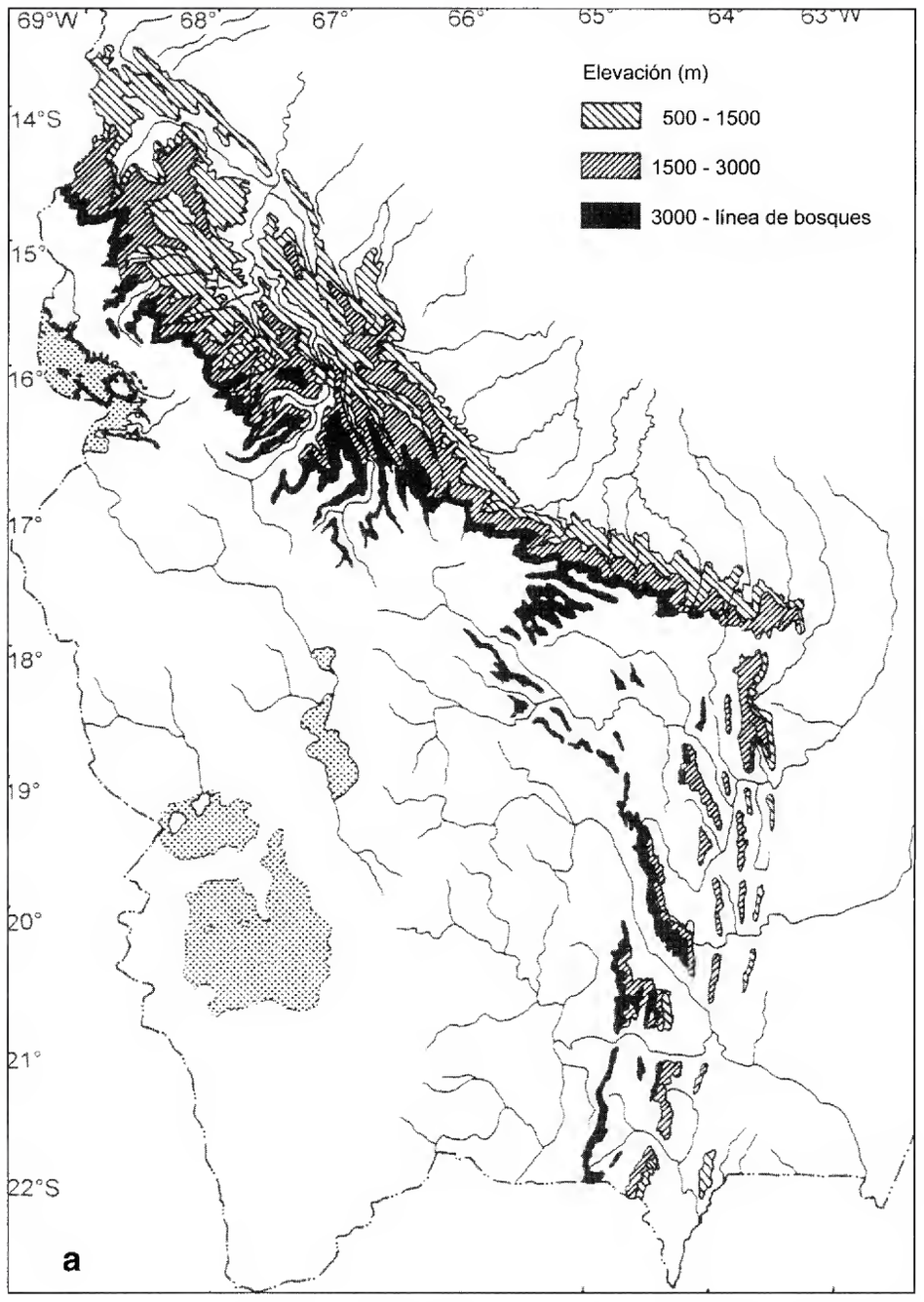


Figure 3.140. Distribution of cloud forests in Bolivia. From Kessler and Beck (2001). Used with permission of Editorial INBio, Santo Domingo de Heredia, Costa Rica.

temperate (e.g., *Podocarpus*) and northern temperate elements (*Alnus*, *Juglans*, *Myrica*, *Prunus*, *Sambucus*) introduced during the climatic cooling of the late Cenozoic. The bosque nublado (cloud forest) association covers 150,000 km^2 (13.7%) and includes about one-half of the plant species of Bolivia. The vegetation on the Altiplano is under the influence of an immensely complex climate system involving dry winds from the west and moist winds rising from the east, and modified by the "elbow" of the Andes Mountains. The elbow presents a right-angle barrier to winds flowing south along the eastern slopes, producing "super wet" areas that may have constituted refugia in the already moist Bolivian lowlands (Chapters 7, 8). The Altiplano also is located in a transition region between climatic events to the north—like the Younger Dryas, Heinrich, and Dansgaard–Oeschger events—and climatic events to the south that are similar but complicated by lag times, and between the Milankovitch variations, which are partly asynchronous between the high latitudes (Chapter 7).

The dry Andean valleys are also influenced by convective air rising from the warm and sparsely vegetated, albedo-reflective valleys. This produces rainfall on the flanking ridges making even less moisture available to the valleys. These dry cuts across the montane forest both fragment the forest and consti-

Figure 3.141. The Atacama Desert of northern coastal Chile. Photograph by J. Arthur Herrick.

tute barriers to the migration of component species depending on their dispersal potential (Killeen, pers. comm., 2005). This conjures up a topographically reverse image of the barriers in the lowlands formed by the Iquitos Arch and with similar implications for speciation.

Chile

Mediterranean climates are characterized by mild temperatures, winter rains, and prolonged dry summers (Thrower & Bradbury, 1977; Kalin Arroyo et al., 1995; Dallman, 1998). In the Mediterranean zone of Chile, the dry season is from August to April and rainfall is 25–100 cm. In the five regions where this climate prevails (around the Mediterranean Basin, South Africa, Australia, California, and Chile), the structure of the vegetation and the many adaptations to prolonged drought are similar, but the composition is different. The most recent and comprehensive summaries of the vegetation of Chile are the *Flora de Chile* (Marticorena & Rodríguez, 1995 et seq.) and an earlier catalog of the vascular plants by Marticorena and Quezada (1985). Gajardo (1994) provides a general survey that includes vegetation maps, color illustrations of representative communities, and tables of climatic data for Chile. The principal plant formations are given in Appendix 1.22. Of particular interest are the desert, and *Fitzroya* (Chile's national tree), *Podocarpus*, *Drimys*, and the *Nothofagus* forests (see Fig. 3.144; Chapter 8, Notes on Some Lineages) that grow in the cool to cold regions of southern Chile within the lower to upper montane broad-leaved forest (bosque lluvioso siempreverde). These trees produce distinctive pollen that is well represented in the fossil record (see Figs. 3.145, 3.146). There is a catalog of the modern pollen and spores of Chile (Heusser, 1971) that also includes illustrations of Late Glacial plant microfossils.

Desert—Except during El Niño years, the Atacama Desert of northern Chile qualifies as hyperarid on all counts—precipitation, evapotranspiration, biotic composition, structure, and adaptations (Fig. 3.141). The MAP is generally below 10 mm, at coastal Antofagasta it is ~0.3 mm, and it essentially never rains in Calama at the upper altitudinal limits of the desert near 2500 m. Salt basins (e.g., the Salar de Atacama) are practically devoid of vegetation. The zone between ~2500 and 3200 m is called the prepuna (MAT ~10° C, MAP 20–70 mm) and supports such plants as *Atriplex imbricata*, *Opuntia camachoi*, and dry annuals. Between 3200 and 3800 m, precipitation increases to 70–150 mm, and the vegetation includes *Chuquiraga*, *Fabiana*, *Junellia seriphioides*, *Lampaya medicinalis*, *Oreocereus leucotrichus*, *Trichocereus atacamensis*, and numerous annual grasses and composites. From 3800 to 4500 m (the upper limit for most vascular plants; MAT 0° C, MAP 150–230 mm), there are grasses (*Festuca orthophylla*, *Jarava frigida*, *Stipa chrysophylla*, *Deyeuxia*) and cushion plants (e.g., *Azorella compacta*).

The limitations to tracing the history of desert and other arid vegetation types have been mentioned earlier. For Chile, the prospects are improving with the discovery of dried plant material protected from wind and El Niño floods in rock crevices. Although the pack rat *Neotoma* does not occur in Chile (the southern limit of its range is in Guatemala; I: pp. 131–137), other rodents, such as the vizcacha and leaf-eared mice, do live among the rocks and gather plant debris for nests. Some of these middens have been dated at 22 Kyr ^{14}C years. For the interval between 16.2 and 10.5 years B.P., they consist of plants presently growing in wetter habitats at higher elevations, and suggest a later trend toward warmer and drier modern conditions (Chapter 7). These data, particularly in the context of information from other lines of inquiry (anthropological records; ENSO events reflected in algal alkenones in marine sediments, I: p. 32), are providing information about the history of an ecosystem poorly represented in traditional fossil assemblages.

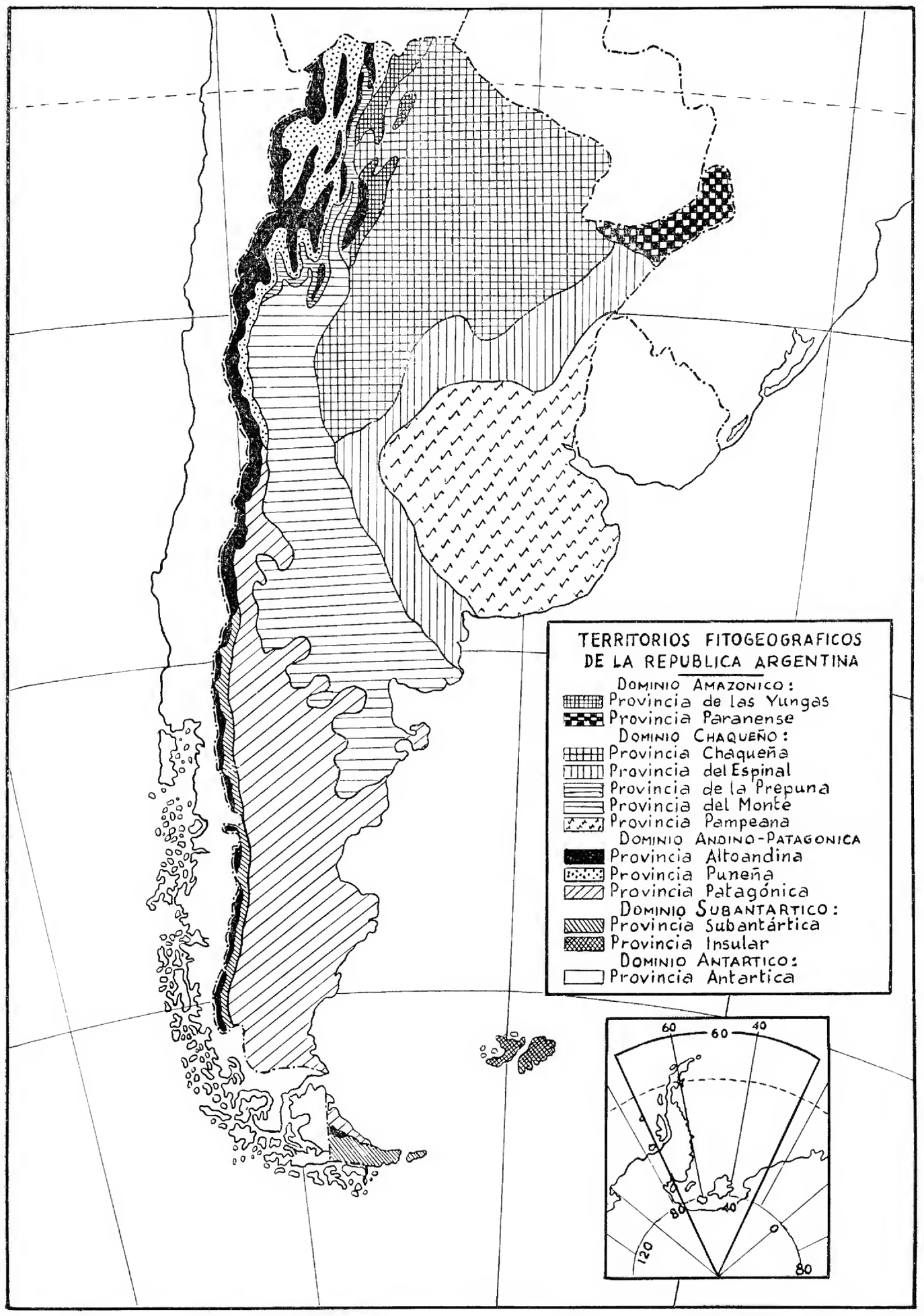


Figure 3.142. Phytogeographic provinces of Argentina. From Cabrera (1971). Used with permission of the Sociedad Argentina de Botanica, Corrientes.

Argentina

The catalog of vascular plants of Argentina (Zuloaga et al., 1994; Zuloaga & Morrone, 1996, 1999) lists 9560 species, including a rich component of Poaceae (1151 species). There are other studies on the genera of seed plants (Hauman, 1984), forest relicts in the mountains of northwestern Argentina (Nores & Cerana, 1990), and invasives (Söyrinki, 1991). Cabrera (1971, 1976) made extensive studies of the vegetation and phytogeography of Argentina, and in his system the vegetation is classified into three regions (Neotropical, Antarctica, oceanica), five dominions, 13 provinces, and various districts (see also Morrone, 2000). These are geographically defined, so most provinces include several community types. They are listed in Appendix 1.23, along with representative species for each province, and their distribution is shown in Fig. 3.142. There are several distinctive biotic provinces in Argentina, such as the Yungas (Provincia de las Yungas; Brown et al., 2001), the grasslands of the Pampas (Provincia Pampeana, Appendix 1.23), and the *Araucaria angustifolia* (paraná pine) forests of the Provincia Paranense (see Fig. 3.175). The latter grow between 500 and 800 m elevation and extend northward into Brazil as far as Minas Gerais, where they occur as scattered populations to 2000 m elevation. The Andean species is *A. araucana* (= *A. imbricata*). Other distinctive Southern Hemisphere gymnosperms in Argentina are *Austrocedrus chilensis* (Pastorino

Figure 3.143. Leaves and flowers of *Schinopsis balansae*. From TROPICOS, photograph by Alwyn Gentry. Used with permission of the Missouri Botanical Garden, St. Louis.

& Gallo, 2002) and *Fitzroya cupressoides* (Premoli et al., 2000). The vegetation of three distinctive regions, the Gran Chaco, Monte, and Patagonia, are discussed below.

Gran Chaco—The vegetation of the Gran Chaco of Argentina is a semiarid tropical dry forest included here in the shrubland/chaparral–woodland–savanna plant formation. The characteristic plants are *Schinopsis balansae* (Fig. 3.143) found in marshes of the eastern plains, *S. quebracho-colorado* in the drier central and western plains, and *S. haenkeana* toward the eastern slopes of the Andes Mountains (Prado, 1993; Martínez Carretero, 2000). In drier or disturbed habitats, the vegetation is a savanna of the grass *Elionurus muticus* with scattered trees of *Prosopis nigra*. Other prominent members of the Gran Chaco savannas are *Spartina argentinensis* and the palm *Copernicia alba*. There are gallery forests of *Arecastrum romanzoffianum*, *Albizia polyantha*, *Banara arguta*, *Crateva tapia*, *Croton urucurana*, *Geoffroea striata*, *Hexachlamys edulis*, *Inga uruguensis*, *Nectandra falcifolia*, and *Peschiera australis*. The Gran Chaco also has river margin forests beyond the limits of flooding supporting *Enterolobium contortisiliquum*, *Ficus luschnathiana*, *Holocalyx balansae*, *Patagonula americana*, *Peltophorum dubium*, *Phytolacca dioica*, *Pisonia aculeata*, *Pouteria gardneriana*, *Ruprechtia laxiflora*, *Sorocea sprucei*, and *Trichilia elegans*. The driest western part of the Gran Chaco consists of *Aspidosperma quebracho-colorado*, *Ceiba*, *Cercidium praecox*, *Cereus bonplandii*, *Cordia glabrata*, *Enterolobium contortisiliquum*, *Geoffroea decorticans*, *Larrea cuneifolia*, *L. divaricata*, *Monvillea cavendishii*, *Pereskia sacharosa*, *Prosopis nigra*, *Zizyphus*, and others that are transitional to the near-desert communities of the Monte.

Monte—A perusal of the plants of the Provincia del Monte (Appendix 1.23) and the dry Uspallata Valley in the Central Andes Mountains (Martínez Carretero, 2000) reveals a number of genera also found in the deserts and semideserts of northern Latin America: *Acacia*, *Caesalpinia*, *Cassia*, *Cercidium*, *Larrea*, *Mimosa*, *Prosopis*, and others. There are numerous examples of plants having extensive more or less continuous geographic ranges throughout Latin America, but the distinctive feature of the Monte vegetation is that many plants are disjunct between the Sonoran Desert and adjacent dry regions of western U.S.–Mexico and the Monte of Argentina (Morello, 1958; Raven, 1963, 1971; Solbrig, 1972). Among the 500 examples of vascular plant genera with this pattern, ~50 (10%) are shared genera, and among the estimated 5000 species common to these two regions, ~150 (2%) represent disjunct pairs (viz., the same or closely related species). The most prominent are *Larrea tridentata* (creosote bush in the Sonoran Desert) and *L. divaricata* (gobernadora or jarilla in Argentina along with *L. cuneifolia* and *L. nitida*); *Prosopis juliflora–P. chilensis* (mesquite-algarrobos); *Celtis pallida* and *C. laevigata–C. spinosa*; *Condalia lycioides* and *C. spathulata–C. microphylla*; and *Zizyphus sonorensis–Z. mistol*. Also found in both regions are *Atamisquea emarginata*, *Caesalpinia gilliesii*, and closely related species of *Cercidium*. For *Larrea*, based on *rbcL* and internal transcribed spacer (ITS) cladistic analysis, the clade including *L. tridentata* and *L. divaricata* is both monophyletic and derived from a common South American ancestor (Lia et al., 2001). Molecular clock evidence suggests arrival and divergence of *L. tridentata* in North America between 8.4 and 4.2 Ma. The oldest fossil record is from the late Pleistocene (18,700 ± 1050 years B.P.; Table 4.1). Explanations for disjunct distributions are generally long-distance dispersal, parallel or convergent evolution, vicariance, or migration through a former connecting arid corridor. One of these (the arid corridor) can be assessed from paleobotanical evidence and will be discussed in Chapter 8. Among the others, long-distance dispersal appears the most likely explanation.

Patagonia—The Pacific coastal vegetation of Patagonia is bog and moorland, and, in sheltered areas with MAP of 800–4000 mm, there are isolated forests of the evergreen *Nothofagus betuloides* (southern beech; Figs. 3.144–3.146). In drier areas, a deciduous species, *N. pumilio*, occurs as part of the mixed woodland with an understory of *Berberis ilicifolia*, *Empetrum rubrum*, *Gunnera magellanica*, and *Senecio acanthifolius*. On the eastern slopes to an elevation of ~500 m, there is a mixture of *N. antarctica* and *N. pumilio* with *Berberis buxifolia*, *Drimys winteri*, *Maytenus magellanica*, and *Pernettya mucronata*. Low shrubs of *Bolax gummifera* and *Empetrum rubrum* grow in open dry areas, and *Sphagnum* bogs form in depressions. Farther to the east, MAP decreases to below 400 mm and the vegetation is steppe (estepa arbustiva árida y estepa arbustiva semiárida; estepas arbustivas áridas with *Junellia tridens*, *Nassauvia glomerulosa*, *N. ulicina*, *N. axillaris*, and *Stillingia patagonica*; estepa arbustiva semiárida with *Larrea ameghinoi*, *L. divaricata*, *Chuquiraga avellanedae*, *Colliguaja*, and *Geoffroea*; Correa, 1969 et seq.). Geological studies of the glaciated landscape and extensive palynological investigations from numerous bog and other sediments have provided considerable information on the Quaternary vegetation of the region (McEwan et al., 1997).

Guianas (Guyana, Suriname, French Guiana)

The vegetation of the Guianas is included in summaries and classifications for tropical American plant formations (Beard, 1944), the Amazon Basin forests (Prance, 1979, 1989), the Guianas as a group (Granville, 1988), and for Guyana

(Davis & Richards, 1933–1934; summary in Richards, 1996, pp. 296–304; Fanshawe, 1952), coastal Suriname (Lindeman, 1953), and French Guiana (Cremers & Hoff, 1990 et seq.; Mori et al., 1997 et seq.; Granville, 2002). The plant communities are familiar from other parts of Latin America and consist of shrubland/chaparral–woodland–savanna (e.g., the Rupununi savanna; abundant *Curatella americana*; Beard, 1953; Heyligers, 1963; van Donselaar, 1969; Teunissen & Wildschut, 1970), mangroves (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, with *Mauritia flexuosa* and *Pterocarpus officinalis*), beach/strand/dune (*Ipomoea pes-caprae*), freshwater herbaceous bog/marsh/swamp (*Cyperus giganteus*, *Typha latifolia*), aquatic (*Utricularia* sp.), lowland tropical rain forest (*Apeiba*, *Ficus*, *Geonoma*, *Heliconia*, *Inga*, *Swartzia*), and lower to upper montane broad-leaved forest. *Mora excelsa* and *M. gonggrijpii*, from an association of marsh forest along rivers, are associated with rain forest plants like *Carapa guianensis*, *Catostemma commune*, *C. fragrans*, *Clathrotropis brachypetala*, *Eperua falcata*, *E. rubiginosa*, *Eschweilera wachenheimii*, *E. sagotiana*, *Macrolobium bifolium*, *Pentaclethra macroloba*, *Pterocarpus officinalis*, *Symphonia globulifera*, *Tabebuia insignis*, *Terminalia dichotoma*, and *Vatairea guianensis* (see Natural Vegetation Map, Guyana Forestry Commission; http://www.forestry.gov.gy/vegmap.htm). The rain forest is transitional to the lower, wettest phase of the montane broad-leaved forest, but it extends from near sea level to ~600 m, MAP is >2000 mm, and there are ~746 species of trees recorded for French Guiana, which is 90,000 km^2 in size (Granville, 1988), or about the size of Maine (86,000 km^2). The classification systems of Granville (1988, 2002) for the vegetation of Guyana and French Guiana, for which the most detailed and recent information is available, are given in Appendix 1.24 along with some representative species. There are two studies on the Tertiary palynology of Guyana and Suriname, but the history of the vegetation is mostly unknown.

Figure 3.144. *Nothofagus betuloides*, Patagonia. From McEwan et al. (1997). Used with permission of ©Trustees of the British Museum.

Paraguay and Uruguay

The Paraguay River divides Paraguay into a northern portion (the Chaco Boreal) and a southern portion (Region Oriental), and the vegetation of both is similar to that of adjacent countries. The dry forest of the Chaco Boreal is part of the Gran Chaco described previously for Argentina (e.g., *Aspidosperma quebracho-blanco*), and the Region Oriental is covered by savanna–grassland (e.g., *Copernicia australis*) like that of Mato Grosso do Sul, Brazil. There is an ongoing flora of Paraguay (Spichiger, 1983 et seq.), a collection of early papers on the vegetation (Chodat & Vischer, 1977), a treatment of the trees and shrubs (Michalowsky, 1953), a study of the plants of the Chaco Boreal (Ramella & Spichiger, 1989), a database for vascular plants (Conservatoire et Jardin Botaniques Ville de Gèneve Web site, http://www.ville-ge.ch/cjb/bd/checklist/index.php), and a series of soil and land use maps (Lopez G. et al., 1995a, b; Meza et al., 1995; Barboza M. et al., 1999). There are few summaries of Uruguayan vegetation (Lombardo, 1964), which is similar to that of the Argentine Pampas, and there is a soils map (Dirección de Suelos y Fertilizantes, 1976). No paleobotanical information is available for Paraguay or Uruguay.

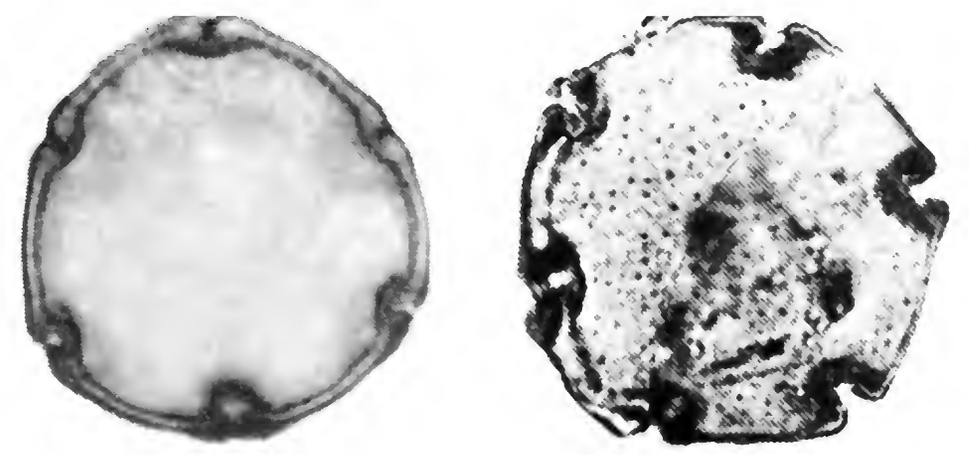


Figure 3.145 (left). Modern pollen of *Nothofagus antarctica*.

Figure 3.146 (right). Fossil pollen of *Nothofagus* (*Nothofagidites cincta*) from the Eocene Río Turbio Formation, Santa Cruz, Argentina. From Romero (1977). Used with permission of Edgardo G. Romero.

Table 3.9. Principal vegetation types of lowland South America, after Prance (1987) and according to the system used here. The lowland Neotropical rain forest is included under Amazonian rain forests on terra firme.

Prance (1987)

Caatinga (tropical thorn scrub)
- Arboreal
- Shrubby
- Parkland

Cerrado (central Brazilian savanna and savanna forest)
- Cerradão = savanna forest
- Campo cerrado = isolated tree savanna
- Campo limpo = parkland savanna

Amazonian savanna
- Savanna on terra firme
- Inundated savanna (campo de várzea)

Transition forests
- Semi-deciduous forest
- Mixed forest with palms
- Babassú forest (pure *Orbignya*)
- Liana forest
- Bamboo forest
- Floodplain open mixed forest

Amazonian rain forests on terra firme
- Lowlands, relatively flat relief, dense forest
- Undulating and submontane relief (<100 m)

White sand formations
- Campina (= open areas on white sand formations)
- Campina forest (campinarana or caatinga Amazônica), and Wallaba (*Eperua*) forest
- Campina rupestre (sandstone rock outcrops)
- Coastal restinga (beach forest)

Inundated forest types
- Swamp forest
  - Permanent swamp forest (white water)
  - Permanent igapó (black or clear water)
  - Periodically flooded forest
    - Mangrove forest (seawater inundation)
  - Tidal várzea (tidal inundation, fresh water)
    - Seasonal várzea (white water)
    - Seasonal igapó (black or clear water)
    - Floodplain forest (flash flooding)

Gallery forests of savanna areas

Montane forest types (>700 m)
- Low montane (to ca. 1000 m)
- Cloud forest (upper montane forest)
- Open montane habitats—subalpine vegetation
- Rocky outcrops (inselbergs)

Secondary forest and agricultural areas

Present Text

Shrubland/chaparral–woodland–savanna
- Caatinga
- Cerrado
- Amazonian savanna
- Transition forests—semi-deciduous forest

Mangrove
- Mangrove forest

Lowland Neotropical rain forest
- Amazonian rain forests on terra firme
- Inundated forest types (except mangrove forest)
- Gallery forests

Lower to upper montane broad-leaved forest
- Transition forests
  - Mixed forest with palms
  - Babassú forest
  - Liana forest
  - Bamboo forest
  - Floodplain open mixed forest
- Montane forest types

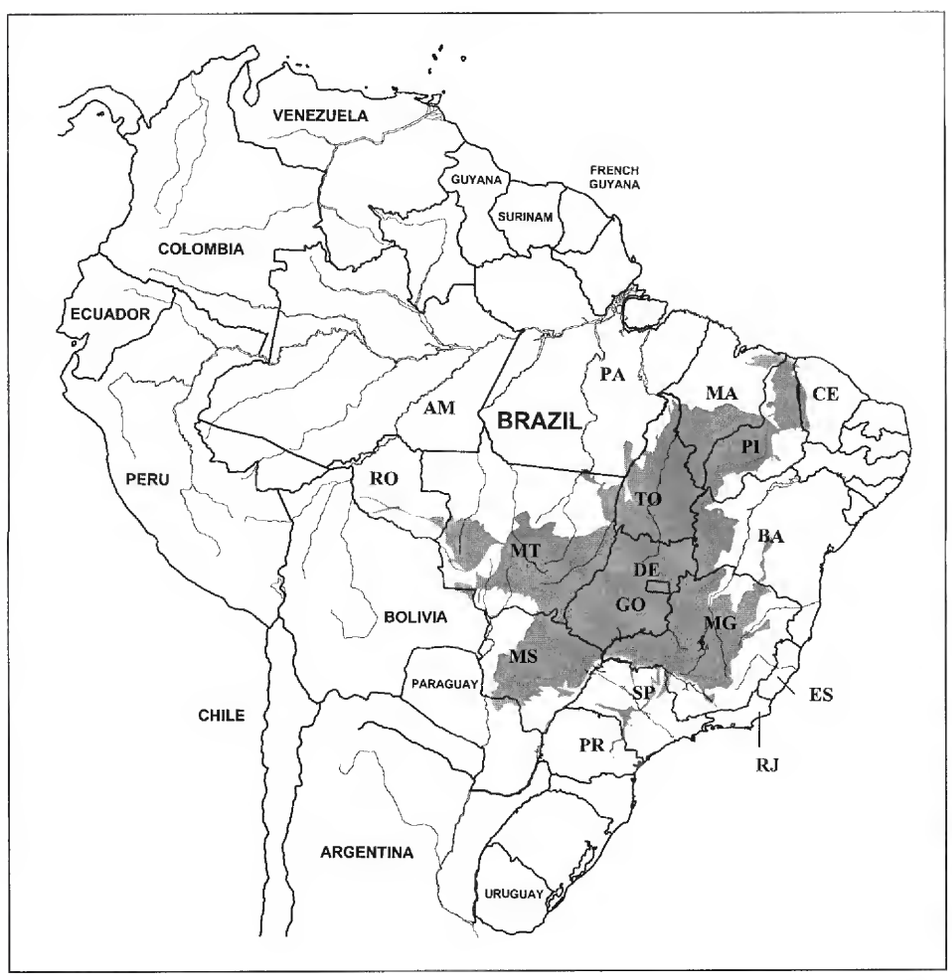


Figure 3.147. Distribution of cerrado vegetation in South America (see Fig. 1.59 for state names). From Oliveira and Marquis (2002). Used with permission of Columbia University Press, New York.

Figure 3.148. Cerrado, Serra do Roncador, Mato Grosso, Brazil. From Eiten (1972). Reprinted by permission from the New York Botanical Garden, Bronx.

Brazil

Ironies

I. "Cash pours in to protect Brazil's rainforests: Brazil is to receive a loan of up to US $1.2 billion from the World Bank over the next four years to help integrate environmental-protection measures into its plans for economic development…to improve environmental management of critical areas such as tropical rainforests and savannah. The destruction of these resources by commercial activities, such as cattle ranching, currently costs the country as much as 4% of its annual gross domestic product." (Nature, 2004, Vol. 431: 9)

Figure 3.149. Location and extent of the Pantanal. From Swarts (2000). Used with permission of Waterland Research Institute, Gouldsboro, Pennsylvania.

Figure 3.150. View of the Pantanal, Nhecolândia. From Por (1995). Used with permission of Kluwer Academic Publishers, Dordrecht, The Netherlands.

II. "Amazon reduced by 10,000 square miles: Deforestation in the Amazon in 2004 was the second worst ever as more rain forest was cleared for soy farms and cattle ranches, according to new figures released by the Brazilian government. Satellite photos and data showed 10,088 square miles of rain forest were destroyed in the 12 months ending in August 2004, the Brazilian Environmental Ministry said. The destruction was nearly 6 percent more than in the same period the year before. Nearly half the total deforestation took place in Mato Grosso state, whose Gov. Blairo Maggi's farming operations are the world's single largest soy producer. Soy is the country's biggest farm export, equal to about $10 billion last year." (MSNBC.com, 19 May 2005; see also Asner et al., 2005)

Brazil covers a vast area of 8,512,000 km^2, compared to 7,678,000 km^2 for conterminous United States, and it includes a vascular flora estimated at 56,000 species compared to ~20,000 species for North America (http://earthtrends.wri.org). The distribution of the principal plant formations is shown on the UNESCO (1980–1981) vegetation map of South America, and for Brazil specifically on the maps of Pires (1973), Kuhlmann (1977), Tosi (1983), Prance and Brown (1987), and IBGE (1993). The Projeto RADAM (1973–1975) and its successor, the Projeto RADAMBrasil (1975–1985), as of 1987 had produced 32 volumes of detailed radar-imaged maps that have been used in numerous projects including the construction of vegetation maps (Veloso, 1966; Veloso et al., 1991; Daly & Prance, 1988).

Several systems exist for classifying the vegetation of Brazil (Ducke & Black, 1953, 1954; Pires & Prance, 1985) and

Figures 3.151 (above), 3.152 (right). *Cyperus*. 3.151—*C. giganteus* in the Pantanal. From Heckman (1998). Used with permission of Kluwer Academic Publishers, Dordrecht, The Netherlands. 3.152—Leaves and flowers of *C. tenuis*, Barro Colorado Island, Panama. From Croat (1978). Used with permission of Stanford University Press, http://www.sup.org.

the lowland tropical communities (Prance, 1987; Table 3.9). Among the informal names used for the plant formations of Brazil and other countries are hylaea, coined by von Humboldt and generally denoting the lowland Neotropical rain forest; mata in Chile meaning shrub, in Venezuela an isolated forest grove, and in Brazil a forest (e.g., mata densa = dense forest; mata aberta = open forest); pirizal, a marsh or community of floating aquatics (*Salvinia*, *Cyperus giganteus* [see Figs. 3.151, 3.152], *Thalia geniculata*, *Cabomba*, *Eichhornia*, *Eleocharis*, *Limnanthemum*, *Nymphaea*, *Sagittaria*); vereda (buritizal) denoting flooded ± pure stands of the palm *Mauritia flexuosa* (see Fig. 3.130); and restinga, sand-dune vegetation (*Byrsonima crassifolia*, *Chrysobalanus icaco*, *Hibiscus tiliaceus* [see Figs. 3.19–3.22], *Ipomoea pes-caprae* [see Fig. 3.23], *Manilkara triflora*). Among the plant formations unique in their composition and/or extensiveness and mostly designated by special names are the cerrado and caatingas, pantanal, lowland Neotropical rain forest, várzea, and Atlantic forest. Remnants are preserved in the 52 national parks shown in the Philips Guides (2002).

Cerrado and caatinga—The complex of vegetation associations known as cerrado is difficult to define precisely, but it may be conceptualized as savanna with transitions to (1) low to medium dry shrubland or dense woodland approaching closed forest, and (2) to more open communities approaching grassland (Novaes Pinto, 1994; Pennington et al., 2000; Oliveira & Marquis, 2002; Gottsberger & Silberbauer-Gottsberger, 2006). Fire is common and most components are either fire tolerant or fire dependent. The name is derived from the Portuguese meaning "closed," and in its denser phases it is nearly impenetrable. Among the characteristic plants are species of *Bowdichia*, *Byrsonima*, *Curatella*, and *Kielmeyera* (Appendix 1.25). There are only a few spiny plants (*Cereus peruvianus*, *Mimosa albolanata*, *Smilax brasiliensis*), so chaparral is not a significant part of the cerrado, and mesic vegetation is confined to outcrops of edaphically richer soils or to gallery forests with elements from the Amazonian forest to the northeast and the Atlantic forest to the east and southeast. MAP is from 750 to 2000 mm, and it is seasonal with a dry period between April and September. Still drier habitats trend toward caatinga, which does have a spiny component, and more moist habitats toward evergreen forest. MAT is 20°–26° C (extremes of –4° to 44° C). The average elevation is 500–600 m, and soil fertility is low. The cerrado occupies western Bahia and Minas Gerais, almost all of Goiás, and eastern Mato Grosso, with extensions into adjacent dry regions (Figs. 3.147, 3.148). It covers ~2 million km^2, or ~22% of the country, and ~50% of that is being modified through human activity. There are an estimated 4400 species of endemic plants, or 1.5% of the Earth's vascular flora (Oliveira & Marquis, 2002).

Warming (1892) made an early study of cerrado vegetation, and recent summaries are provided by Goodland (1970, 1971), Ratter et al. (1973), Goodland and Ferri (1979), Ribeiro and Walter (1998), Castro et al. (1999), Furley (1999), Guarim et al. (2000), Filgueiras (2002), and Oliveira-Filho and Ratter (2002). Representative plants of the cerrado are given in Appendix 1.25, and more extensive lists are provided by Filgueiras and Pereira (1994) and Castro et al. (1999) and for the Federal District by Cavalcanti and Ramos (2001). The terminology for describing the cerrado can be formidable, and it is not made easier by the fact that "cerrado" is used both sensu lato for the overall vegetation, and sensu stricto for one of its component associations. Five principal types are generally recognized. In the treatment of Eiten (1972, 1978), closed cerrado denotes ~60% or more tree cover; open cerrado 10%–60%; and sparse cerrado less than 10%. Tall trees are those 20 m or more in height, medium 7–20 m, and low less than 7 m. Using these definitions, the five types are (1) cerradão, with trees that are densely spaced, tall but some of medium height, and with a crown cover that is mostly closed but down to ~30%–40% (viz., it is the most dense, tallest, and forest-like); (2) cerrado,

with trees less densely spaced, mostly medium but some low in height, and with a crown cover of 30%–40% but ranging to nearly closed (viz., it is less tall and dense); (3) campo cerrado, with trees that are mostly low and with a crown cover that is usually <30%–40% (near-savanna); (4) campo limpo ("clean," meaning essentially devoid of trees; near-grassland that can be seasonally inundated); and (5) campo rupestre (on extensive rocky outcrops with nutrient-poor soils; Stannard, 1995). A new system is being developed by Ribeiro and Walter (1998). The campo rupestre is found between 800 and 2000 m, and clouds from the Atlantic Ocean provide the principal source of moisture in the form of rain or dew (Harley & Simmons, 1986). Among its notable features are the candelabra-like branching of many components, cruciate leaf arrangement (thick, short, close-set leaves arranged in four ranks along the branch or stem, so that when viewed from above, the branch or stem appears cross-shaped in outline), a rocky substrate, and high endemism. Other features of the campo rupestre are its heath-like aspect, and the many vellozias and orchids that impart a special beauty.

Conditions are drier to the northeast toward the Brazilian Highlands, and the vegetation changes to caatinga. This association includes the driest phases of the cerrado, deciduous thorn scrub, and near-desert communities. Plants with spines are prominent, and much of the vegetation is a chaparral. Within the caatinga, there are fragmented enclaves of more mesic montane forests at elevations between 600 and 1000 m (e.g., in the Borborema Highlands of Pernambuco state; Nogueira Rodal, 2002). The principal borders in northeastern Brazil between cerrado and caatinga are in western Bahia and in northwestern Minas Gerais. In southwestern Brazil, the contact between the cerrado and the chaco is along the border with Bolivia and Paraguay into Argentina. This arc-like configuration of caatingas, cerrado, and chaco forms the principal dry vegetation of northern South America (Prado & Gibbs, 1993; Prado, 2000). Species in moist habitats within and adjacent to this arc constitute populations and preadapted elements available to expand and coalesce with changes toward more humid climate.

Figure 3.153. Leaf of *Victoria amazonica*, Manaus, Brazil. Photograph by J. Arthur Herrick.

Figure 3.154. Large leaf of *Xanthosoma robustum*, UNAM Tropical Biological Station, Catemaco, Veracruz, Mexico. From UNAM.

The natural versus anthropogenic origin of the cerrado, and the role of fire in its maintenance, is unsettled. It is agreed that the community is a result of the interaction between climate (warm, moderately dry and seasonal), soil (sterile), fire (frequent), and more recently, human disturbance. It is also a product of environmental change, especially the dry intervals of the Late Tertiary and Quaternary periods. The limited paleobotanical evidence from this environment must be augmented by independent geological and climatological information to infer the history of the cerrado ecosystem (Chapter 7). There is a substantial literature on the spores and pollen of modern cerrado plants, and references through about 1985 are part of the bibliographies mentioned in the Prologue.

Pantanal (Figs. 3.149, 3.150)—The vegetation of the Pantanal consists of aquatic communities, sedge marshes (*Cyperus giganteus*, Figs. 3.151, 3.152), and swamp forests in the lower, permanently inundated parts; seasonally flooded grassland on much of the alluvial plain; and dry savanna (cerrado elements), dry forest (chaco elements; Prado et al., 1992; Heckman, 1998), and lakes with aquatic and marsh ecosystems scattered on the elevated erosional features and ancient deltas. Rainfall decreases to the west and the vegetation merges with semiarid forests of the Gran Chaco of Argentina. There are gallery forests bordering the rivers and connecting the Amazonian and Atlantic moist forests across the cerrado (Junk & da Silva, 1995; Oliveira-Filho & Ratter, 1995). Adamoli (1986) recognizes four phytogeographic provinces within the Pantanal ecosystem: (1) chaco along the western and southern margins, (2) cerrado (savannas and woodlands of Brazil, the most extensive province), (3) peri-Amazonia (semi-deciduous moist forests extending along river valleys with affinities to the north, and (4) Atlantic (semi-deciduous moist forests extending along river valleys with affinities to the east). Prance and Schaller (1982) add another category—"widespread" Neotropical plants. There are also balseiras (camalotes), called "embalsados" in Argentina

Figure 3.155. Buttressed tree of *Bombacopsis fendleri* with lianas, Barro Colorado Island, Panama.

and "batumes" in Paraguay, which are floating mats of plants up to several meters in diameter composed mostly of *Salvinia auriculata*, *Eichhornia crassipes*, and/or *Pistia stratiotes*. They may fuse into larger masses, become lodged on rooted macrophytes or at river bends into semi-stationary plant islands, develop a secondary vegetation and fauna, fragment, and float down the Paraguay River, with their faunal passengers (including an occasional jaguar, *Panthera onca*, or capybara, *Hydrochoerus hydrochaeris*) to the Paraná and La Plata rivers into the Atlantic Ocean.

Another unusual feature of the Pantanal ecosystem is the murundu islands. These are small mounds 1–2 m high built by termites (*Rotunditermes bragantinus*) or leaf-cutter ants (*Atta* or *Acromyrmex*) in the inundated cerrado. They may cover 80% of the ground surface and are evenly spaced, reflecting the territoriality of the insect colonies. One of three species of trees commonly sit atop these mounts—*Tabebuia aurea*, *T. caraiba*, and more rarely *Vochysia rufa*. The value of murundu islands in the Pantanal is in providing a place of lodgment for the trees, protecting the tree roots from waterlogging, providing wood and leaves for the termites and ants, and serving as a dry refuge for trees during extended, multi-year periods of flooding.

Urban (1902) provides an account of the early botanical collectors in the Pantanal including the redoubtable Count Georg Heinrich von Langsdorff (1774–1852). He conducted expeditions between 1824 and 1829 with botanist Ludwig Riedel, under the patronage of the czar of Russia, went mad and died, and his collections were mostly lost or unstudied. Another picturesque figure is Theodore Roosevelt, who visited the Pantanal in 1913. Studies of the vegetation were made by Hoehne (1923, 1936), Veloso (1947), Ratter et al. (1988), and Dubs (1994), and modern pollen types recovered from honey made from Pantanal plants are mentioned by Chaves and Barth (1988, 1989). The prominent plants of the Pantanal are given in Appendix 1.26, and a more extensive list is provided

Figure 3.156. Epiphytes, Manaus, Brazil. Photograph by J. Arthur Herrick.

by Prance and Schaller (1982).

Conditions in the Pantanal vary widely from season to season, due primarily to the amounts of water entering the basin. Among the biological consequences of this unpredictability for the fauna are periodic dominance of different organisms, generalized food preferences, little territoriality, and low endemism. Prance and Schaller (1982) mention only two endemic plants from the Pantanal—*Coccoloba cujabensis* (Polygonaceae) and *Mentzelia corumbaensis* (Loasaceae). As noted by Por (1995, p. 39), "The present conditions are too fluctuating on a yearly and a secular basis, and they were probably even more so in the longer range of the Pleistocene climatic history. Perhaps with the exception of the isolated old hills [with their cave fauna], there has never been an environmental stability and a definition of isolated areas conducive to in situ speciation."

Lowland Neotropical rain forest (Amazon forest, Atlantic forest, várzea association; Bermingham et al., 2005; Morley, 2000; Osborne, 2000)—

> "…the most remarkable expression of nature to grace the surface of the planet in four billion years of life's history." (Myers, 1991)

This plant formation is found in the lowlands mostly between ~10°N and 10°S on relatively level terrane. Temperatures are uniformly high (mean at least 20° C, average 24° C, coldest month mean [June–August] at least 18° C, warmest month mean [October–April] 28°–29° C), and there is no pronounced or extended cold period. The MAP is uniformly high (~1800–5000 mm/yr to a maximum of >11,000 mm/yr) without a pronounced dry period, radiation levels are high during the long cloudless intervals, and the soils are sterile (frequently lateritic) with a dense litter cover and rapid recycling of organic matter. The climatic parameters can be broadly quantified as no more than ~3° C difference between the average cold month and average warm month temperature, and the three driest months (25% of the year) receive at least 18% of the annual rainfall. There have been attempts to more precisely define the climate that supports tropical rain forest vegetation, such as in the Holdridge life zone classification discussed earlier. The Thornthwaite (1948) system estimates evaporation, precipitation, and day length to formulate a series of water balance figures. The numerous equations create an impression of mathematical precision, but when the areas delimited are compared with the actual distribution of tropical vegetation, the correlation is not that close. In the Köppen (1918, 1936) system the climate of the lowland Neotropical rain forest is designated Af, meaning hot, humid, without a dry season, and a MAP >1300 mm. The dry month precipitation limit is

Figure 3.157. Aerial view of the lowland Neotropical rain forest, Ecuador. Photograph by J. Arthur Herrick.

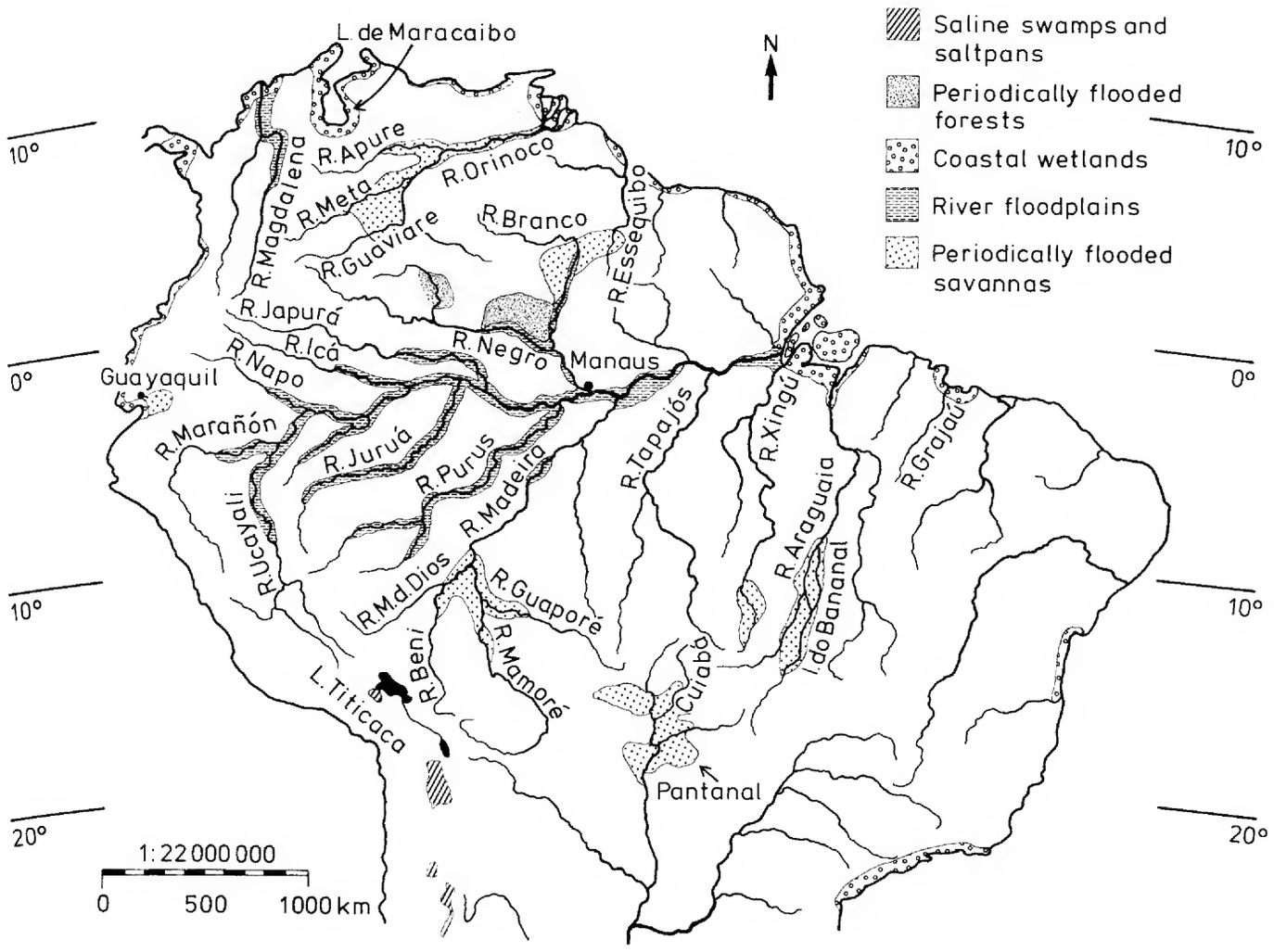


Figure 3.158. Distribution of várzea vegetation in South America. From Junk (1997). Used with permission of Springer Verlag, Berlin.

set at 60–65 mm, but that is too low, and Beard (1944) found that 100 mm was in better accord with the occurrence of rain forest. However, the variables, subvariables, compensations, and positive and negative feedbacks of humidity, cloud cover, wind, soil, topography, temperature, and rainfall have rendered a precise definition elusive, and the general characterization of tropical rain forest climates given above is better suited for present purposes. Climate and related topics with reference to the limnology of Amazonia are presented by Sioli (1984).

There is a syndrome of biological features associated with lowland Neotropical rain forest plants. These are a prominence of angiosperms, especially Fabaceae (Burnham & Johnson, 2004, fig. 2); large size (Figs. 3.153, 3.154; tallest trees 45–55 m to a maximum of ~60 m); buttressing (in compensation for the shallow root system required by rapid recycling of organic matter; Fig. 3.155); numerous lianas (in response to reduced light below the canopy, and competition for space and the nutrients necessary for producing large biomass; "twiners entwining twiners," Charles Darwin, *Voyage of the Beagle*; Fig. 3.155); epiphytes (Fig. 3.156); many evergreen trees (i.e., no one period of synchronous leaf fall); leaves mostly large, thin textured, entire margined, and many with drip-tips; a prominence of animal (especially insect) pollination; and an unexcelled level of biodiversity (Gentry & Dodson, 1987; Fig. 3.157). A sense of the richness of the vegetation is evident from the figures compiled by A. H. Gentry (1982) for the average number of plant species in 1000-m^2 plots for the temperate zone (three sites in the Ozark Mountains of Missouri)—23; dry forest (five sites in Venezuela and Costa Rica)—63; moist tropical forest (three sites in Brazil and Panama)—109; wet tropical forest (two sites in Ecuador and Panama)—143; and pluvial tropical forest (Tutunendo, Colombia)—~258. There is also mass flowering in some groups (e.g., bamboos) and cauliflory (fruits borne directly on the stem; e.g., *Crescentia cujete*, cannonball tree). An earlier view that the tree canopy is typically stratified into three layers has proved too broad a generalization (Richards, 1996). Another changed attitude is that history is irrelevant to understanding tropical diversity because competition has such a rapid effect, compared to climate and geologic changes, that it overrides past events. In reference to Africa, Richards (1952, pp. 230–231) notes "whatever the true explanation for the poverty of the African rain forest, it can hardly be due to any ecological factor operating at the present day" (Bermingham & Dick, 2005).

Figure 3.160. *Salix humboldtiana* on sand bar of várzea in Brazil. From Junk (1997). Used with permission of Springer Verlag, Berlin.

Figure 3.159. Várzea vegetation along the lower Rio Solimões near the mouth of the Rio Negro, Brazil. From Sioli (1984). Used with permission of Dr. W. Junk Publishers, Dordrecht, The Netherlands.

The monumental 15-volume *Flora Brasiliensis* published by Martius (1840–1906) includes ~20,000 species of which 5939 were new. More recent regional treatments include those from Cabrera and Zardini (1978), Lorenzi (1992), Parrotta et al. (1995), Stannard (1995), and Dubs (1998). The Minimum Critical Size of Ecosystems (MCSE) study site near Manaus (Lovejoy & Bierregaard, 1990) was one of the four Neotropical rain forests discussed in Gentry (1990), and the Reserva Florestal Adolpho Ducke is at nearby Manaus (Prance, 1990). A list reflecting the diversity of the lowland Neotropical rain

forest throughout its range is not feasible. As an example of the vegetation from one region, a list of rain forest species from San Carlos de Río Negro in southwestern Venezuela near the border with Brazil is given in Appendix 1.27.

Várzea—This is the floodplain along the white-water rivers of the Amazon Basin (igapó is the floodplain along the black-water rivers; Irion et al., 1997; Figs. 3.158–3.162). Although it constitutes only ~2% of the basin (Fig. 3.158), the várzea is a highly productive ecosystem because the alluvial soils are replenished each year by flooding. During major cycles, the water may rise up to 13 m, persist for 300 days in some years, and deposit 1.5 m of new sediment. In this specialized fluctuating habitat, average diversity is reduced from >200 tree species/ha in the uplands to <100 on the floodplains, and a single species, often a palm (*Astrocaryum jauari*, *A. murumuru*, *Echinochloa polystachya*, *Euterpe oleracea*, *Manicaria saccifera*, *Mauritia flexuosa* [see Fig. 3.130], *Oenocarpus bataua*, *Phytelephas tenuicaulis*, *Raphia taedigera*, or *Socratea exorrhiza*; Kahn & Henderson, 1999), may number >100 individuals/ha. In structure the várzea has a somewhat lower, more open canopy than the upland forest, and it includes a number of large-diameter trees (Peters, 1999). An important component is *Virola surinamensis* (Fig. 3.163), and more than 350 sawmills in the Amazon Basin process ~700,000 m^3 of wood from this tree annually (Anderson et al., 1999). Other prominent trees of the várzea and adjacent lowland Neotropical rain forest are *Alchornea triplinervia*, *Anacardium occidentale* (cashew, Figs. 3.164–3.168; Manchester et al., 2007), *Calophyllum brasiliense*, *Carapa guianensis*, *Cedrelinga cateniformis*, *Ceiba pentandra*, *Cordia nodosa*, *Crudia amazonica* (Figs. 3.169–3.171), *Ficus maxima*, *Guarea guidonia*, *Hernandia* sp., *Hura crepitans*, *Luehea cymulosa*, *Macrolobium bifolium*, *Maquira coriacea*, *Ocotea cymbarum*, *Pithecellobium corymbosum*, *Platymiscium ulei*, *Pseudobombax munguba*, *Sapium hippomane*, *Sterculia elata*, *Triplaris weigeltiana*, *Vatairea guianensis*, *Warscewiczia coccinea*, and *Xylopia calophylla*. The composition, ecology, and sustained management of the várzea are discussed in Prance (1979), Piers and Prance (1985; Balslev et al., 1987), Campbell et al. (1986, 1992), Junk (1997; Junk et al., 2000), Worbes (1997), Padoch et al. (1999), and Jardim et al. (2001).

The várzea is of potential importance to studies on vegetational history because the sediment load includes spores and pollen from many entomophilous species, normally underrepresented in other settings, that are brought into the waters by outwashing and deposited in the deltas of the Amazonian rivers. However, disentangling várzea from other lowland forest types in a fossil assemblage is difficult and depends upon identifying the pollen of palm and other species characteristic of the várzea. This is theoretically possible because the pollen of several palms and other várzea plants is distinctive at the generic level. Distinguishing the community, however, requires familiarity with the composition, arrangement, and pollen signatures of the modern community, associations, and phases of the várzea, and those of the surrounding vegetation; and dealing with the significant limitations of palynology for community reconstructions in this depositional setting (e.g., redeposition, differential production, transport, preservation).

Figure 3.161. Igapó (black-water) woody várzea, beginning of inundation, Rio Cuieiras, lower Rio Negro, Brazil. From Sioli (1984). Used with permission of Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Figure 3.162. Herbaceous várzea. From Junk and Piedade (1997) in Junk (1997). Used with permission of Springer Verlag, Berlin.

Figure 3.163. Leaves and flowers of *Virola* sp., Ecuador. From TROPICOS, photograph by Alwyn Gentry. Used with permission of the Missouri Botanical Garden, St. Louis.

Figure 3.164. Leaves and fruits of *Anacardium occidentale*. From TROPICOS, photograph by W. Pohl. Used with permission of the Missouri Botanical Garden, St. Louis.

Figures 3.165–3.167. Modern pollen of *Anacardium occidentale*. 3.165 (left)—Equatorial view. 3.166 (center)—Polar view, margin. 3.167 (right)—Polar view, surface.

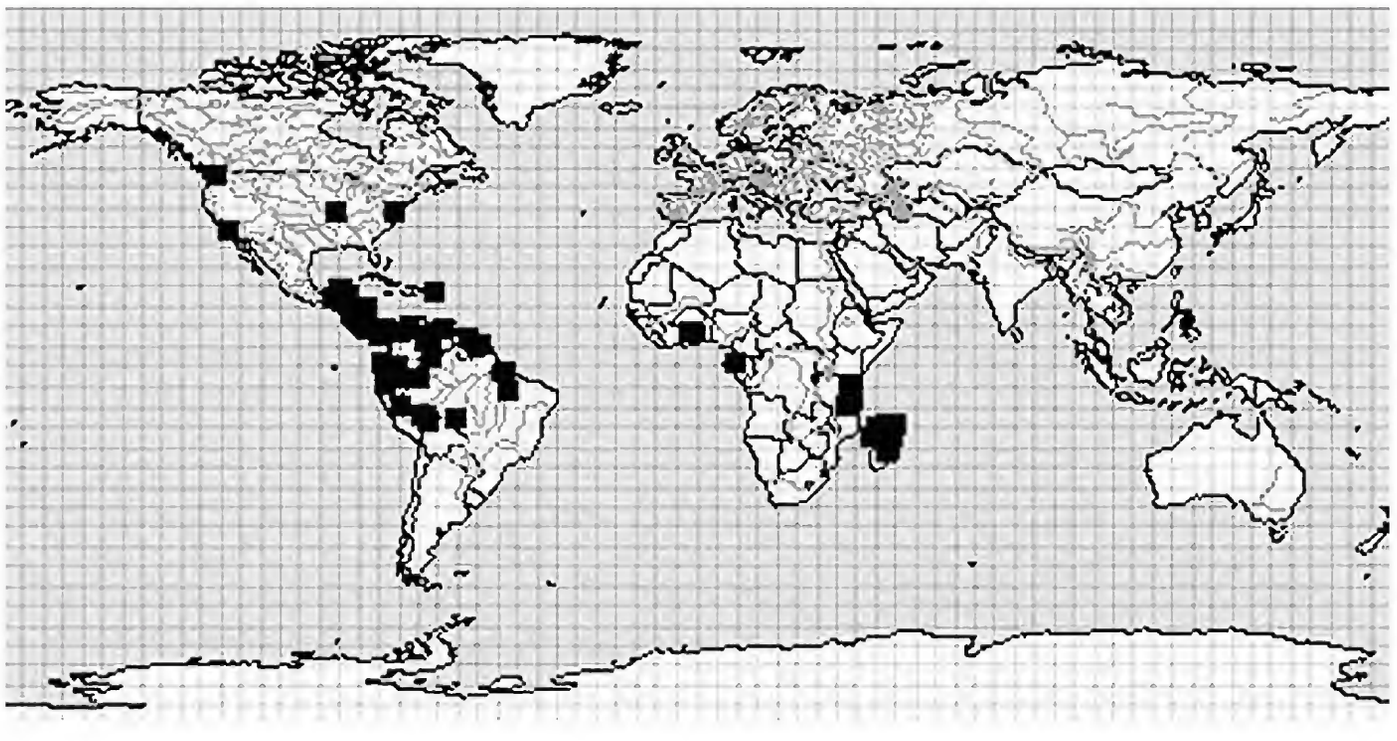


Figure 3.168. Distribution of *Anacardium occidentale*. The species is native to the Neotropics and widely cultivated elsewhere. From TROPICOS. Used with permission of the Missouri Botanical Garden, St. Louis.

Atlantic forest—

"The young Darwin has his first experience there with the tropical fauna and flora. In 1836 on his way home on the *Beagle* Darwin visited Bahia for the second time and had a strange premonition when he wrote: 'In my last walk, I stopped again and again to gaze on these beauties, and endeavoured to fix in my mind for ever, an impression which I knew sooner or later must fail…the thousand beauties which unite these into one perfect scene must fade away; yet they will leave, like a tale heard in childhood, a picture full of indistinct, but most beautiful figures.' Not even the smallest remainder of a forest survives where once Darwin stood." (Por, 1992)

Figure 3.170. Modern pollen of *Crudia amazonica.*

Figure 3.171. Fossil pollen of *Crudia* from the Oligo–Miocene La Quinta Formation, Chiapas, Mexico.

The Brazilian Highlands and its dry vegetation along the crests flanking the Rio São Francisco, including cerrado and caatinga, separate the Amazon forest from the Atlantic forest (Figs. 3.172–3.174; Galindo-Leal & Gusmão-Câmara, 2003). At the species level, the two are relatively distinct. In one study (Mori et al., 1981), only 34.7% of the tree species were common to the two regions, implying a substantial period of separation for many of the components. The Atlantic forest consists of the moist Atlantic semi-deciduous forest on the eastern slopes of the highlands and the wet Atlantic rain forest extending ~300 km inland along the coast (Morellato & Haddad, 2000; Oliveira-Filho & Fontes, 2000). There are swamp forests in the lowlands and open thickets on rocky outcrops in the valleys and highlands forming the usual mosaic of vegetation in a physiographically diverse landscape (Scarano, 2002). The southern boundary of the Atlantic forest is in northeastern Argentina, where one transition is (was) with the former *Araucaria angustifolia* forest of the Provincia Paranense (Appendix 1.23; Fig. 3.175). Less than 10%, and perhaps closer to 5%, of the original 1 million km^2 of the Atlantic rain forest remains (Fig. 3.172) because conditions are ideal for the cultivation of *Hevea brasiliensis* (rubber) and *Theobroma cacao* (cocoa), the harvesting of timber (e.g., *Astronium concinnum*, *Cedrela odorata*, *Dalbergia nigra*, *Plathymenia foliolosa*), the extraction of dye for textiles, the manufacture of bows for musical instruments from *Caesalpinia echinata* (pernambuco or pau-brazil; Mori et al., 1983), and the production of a hyper-caffeine drink (guaraná) from the seeds of *Paullinia cupana.* To the uninitiated, guaraná imparts a shocking red color to the urine. In addition to 500 years of unplanned and unrestrained exploitation dating from the early Portuguese settlement, there are now more than 1.5 million people living in 3000 villages and cities in the former Atlantic forest in addition to the population centers of São Paulo (>10 million people, 15 million in Greater São Paulo) and Rio de Janeiro (>6 to 11–12 million; Morellato & Haddad, 2000).

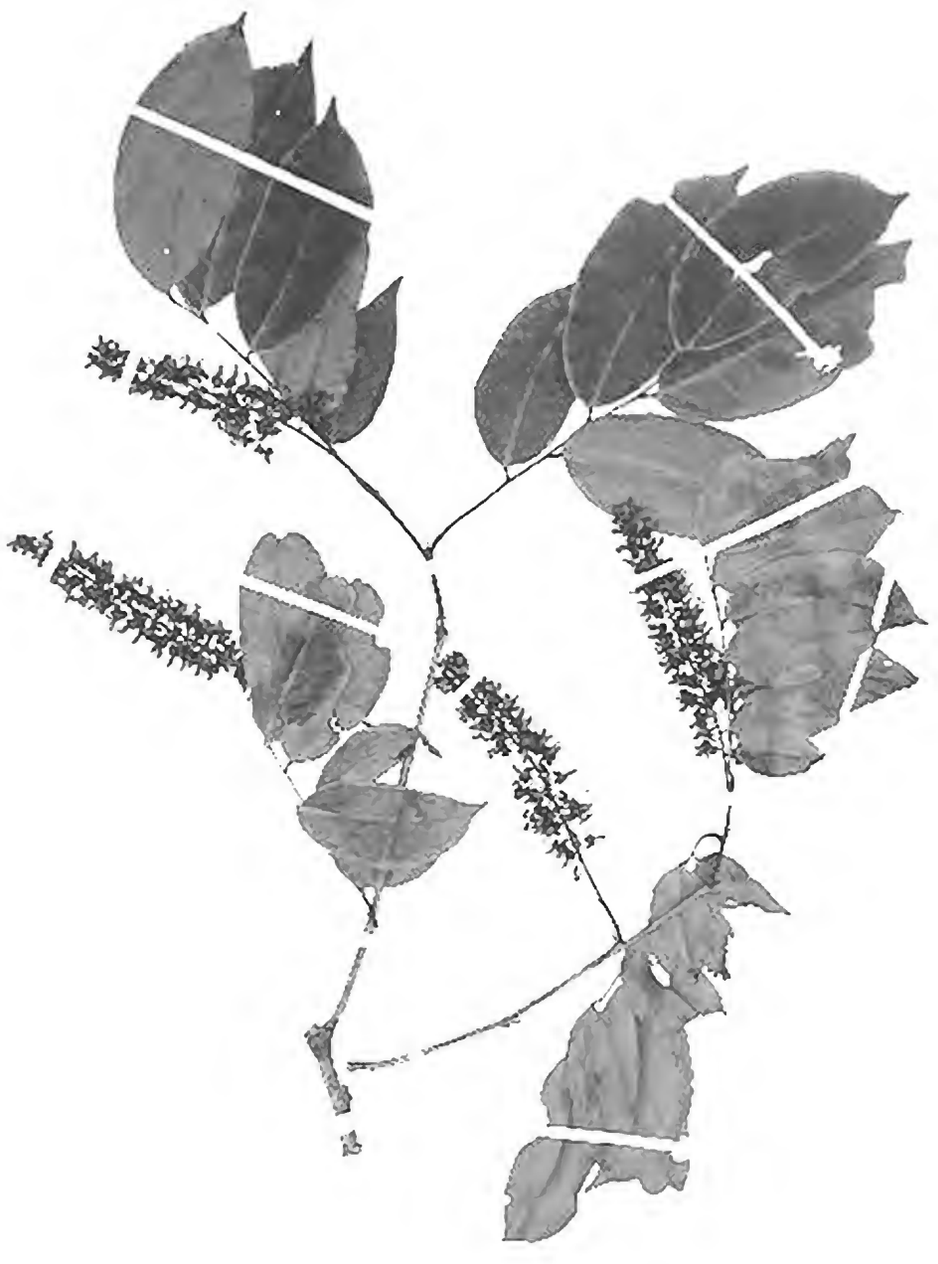


Figure 3.169. Leaves and flowers of *Crudia glaberrima.* From Virtual Tree Guide of the Guianas, Biology University of Utrecht, The Netherlands. Used with permission of Biology University of Utrecht.

Of 127 species of trees studied from the moist forests of eastern Brazil, Mori et al. (1981) found 68 (53.5%) were endemic, and the percentage for overall endemism in the vegetation is about the same. Reviews include lists of plant species for the Atlantic forests (Mori et al., 1983; Oliveira-Filho & Fontes, 2000); an online catalog of plant species of eastern Brazil (Wayt Thomas; the C.V. Starr Virtual Herbarium at NYBG, http://sciweb.nybg.org/science2/hcol/sebc/sebcindex2.asp); a vegetation map for Bahia (Gouvêa et al., 1976); a flora of the Pico das Almas (Stannard, 1995); and a florula of Mucugê (Harley & Simmons, 1986). Among the prominent plants of

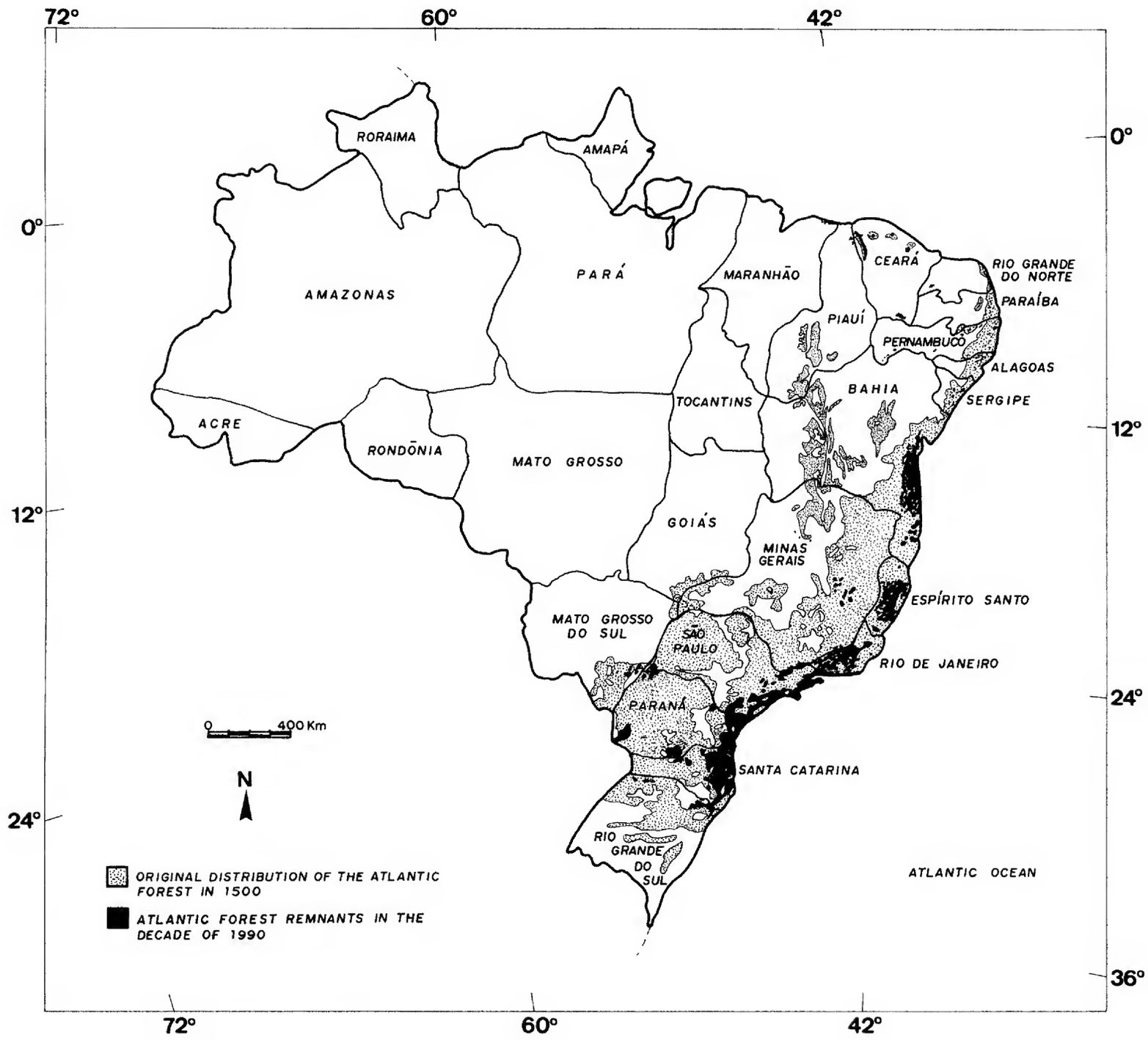


Figure 3.172. Former (~1500 A.D., grey) and modern (1990s, black) extent of the Atlantic rain forest. From Morellato and Haddad (2000), In: The Brazilian Atlantic Forest, Biotropica (Special Issue) 32: 788, Fig. 2. Used with permission of the Association for Tropical Biology (Biotropica), Lawrence, Kansas.

the Atlantic forest are the tree fern *Dicksonia sellowiana*, the gymnosperm *Podocarpus lambertii*, and *Arapatiella psilophylla*, *Buchenavia grandis*, *Dialium guianense*, *Diploon cuspidatum*, *Drimys winteri*, *Ecclinusa ramiflora*, *Eriotheca macrophylla*, *Eschweilera*, *Ilex paraguariensis*, *Licania hoehnei*, *L. micrantha*, *L. salzmannii*, *Luehea paniculata*, *Manilkara salzmannii*, *Nectandra nitidula*, *Ocotea pulchella*, *Simira rubra*, *Sprucella* sp., and *Virola officinalis*. The remnants of the Atlantic forest are quasi-protected by a national patrimony passed in 1990 and a presidential decree issued in 1990, and in the Monte Pascoal National Park (established in 1961 with 22,500 ha; 8500 were ceded to the Pataxó Indians), the Linhares Reserve of the Companhia Vale do Rio Doce, and at the Pau Brasil Ecological Station.

There is no information on the Late Cretaceous or Tertiary vegetation of the Atlantic forest, but a study of paleobotanical interest on the leaf physiognomy of a southern Bahia forest quantifies the familiar association between moderate- to large-size leaves with entire margins and tropical climates (I: pp. 124–128). Among the species examined, 96.6% had entire-margined leaves, and size of class distributions were leptophyll (1.2%), microphyll (14.7%), mesophyll (78.5%), macrophyll (5.1%), and megaphyll (0.6%; Mori et al., 1983). There is an atlas and manual of Amazonian pollen (Colinvaux et al., 1999), and some information on the Late Glacial and Holocene history of the Atlantic forest (Chapter 7).

Summary

This characterization of the vegetation of Latin America is organized around 12 plant formations recognized for purposes of tracing terrestrial vegetational, environmental, biogeographical, and lineage history during the time interval of the Late Cretaceous through the Holocene. An effort to develop a feel for the types of vegetation, their composition as defined by the prominent components, ecological parameters, affinities with other geographic areas and communities, and their arrangement over the landscape may seem somewhat ethereal. Nonetheless, until such an overall impression is achieved, it may be possible to compile lists of fossils for particular times

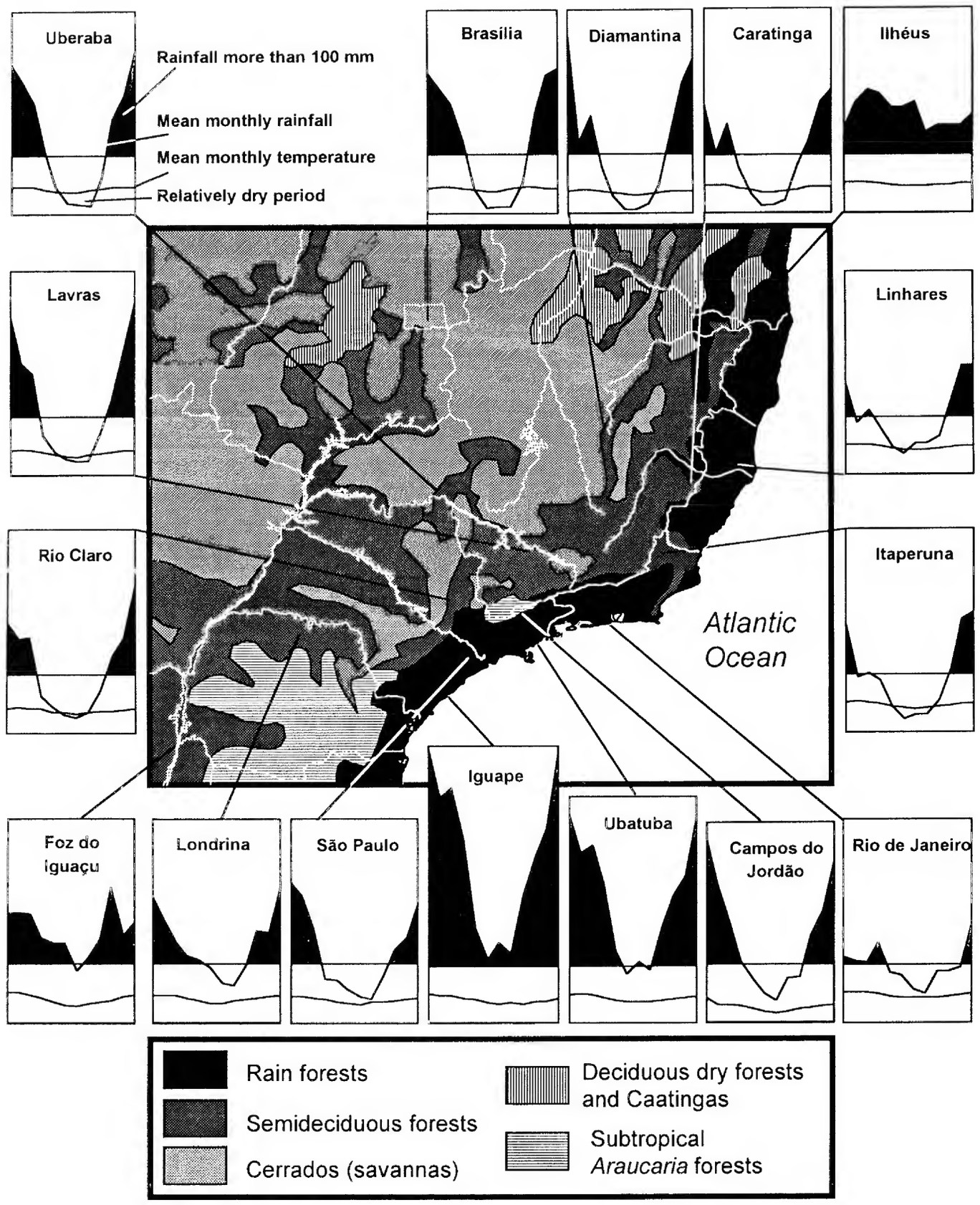


Figure 3.173. Map of southeastern Brazil showing distribution of the Atlantic rain forest and other vegetation types, with Walter climatograms for selected sites. From Oliveira-Filho and Fontes (2000), In: L. P. C. Morellato and C. F. B. Haddad (eds.), The Brazilian Atlantic Forest, Biotropica (Special Issue) 32: 795, Fig. 1. Used with permission of the Association for Tropical Biology, Lawrence, Kansas.

and places, but the interpretation of the data will likely be static and limited. As noted earlier, an introduction to Latin American vegetation for the general reader can be gained in several ways. One is to review selected figures in the text that illustrate the 12 plant formations proposed for this introductory encounter. These include:

Desert—Figs. 3.4–3.7, 3.10, 3.128, 3.141
Shrubland/chaparral–woodland–savanna—Figs. 3.11, 3.88, 3.129, 3.148 (cerrado)
Grassland—Fig. 3.16
Mangrove—Figs. 3.18, 3.92
Beach/strand/dune—Fig. 3.23
Freshwater herbaceous bog/marsh/swamp—Figs. 3.24, 3.25, 3.150 (pantanal)
Aquatic—Figs. 3.89, 3.153
Lowland Neotropical rain forest—Figs. 3.26, 3.28. 3.59 (transitional), 3.93, 3.155, 3.174 (Atlantic forest)
Lower to upper montane broad-leaved forest—Figs. 3.27, 3.36, 3.58 (transitional), 3.77 (transitional), 3.132 (transitional), 3.144 (*Nothofagus*, southern beech), 3.175 (*Araucaria*)
Coniferous forest—Figs. 3.37, 3.41, 3.42, 3.43, 3.60
Alpine tundra (páramo)—Figs. 3.135–3.137
Tundra—See Fig. 1.56

Figure 3.174. The Atlantic rain forest. From Por (1992). Used with permission of Backhuys Publishers, The Netherlands.

Figure 3.175. *Araucaria angustifolia* (paraná pine) in Aparados da Serra National Park, Brazil. From Por (1992). Used with permission of Backhuys Publishers, The Netherlands.

A second source is the illustrations of the plant formations and representative species for each formation from the Web sites mentioned earlier. The appendices give other characteristic plants, and reference to the climatograms provides an indication of the climates under which they grow. An overall sense of the vegetation of Latin America can be gained by periodically reviewing these sources, and they can provide a level of familiarity that is satisfactory for an introduction to the flora. Deeper experience with the intricacies of the modern vegetation will bring another dimension to the study of vegetation history, namely a sense of when it is appropriate to go beyond the limitations of methods and data in making paleoenvironmental, lineage, or biogeographic reconstructions (viz., to speculate), and when it is prudent to acknowledge the limitations and be more conservative. The paleobotanical data presented in the following chapters provide working snapshots of plants, communities, environments, times, and places as one component toward achieving an ecosystem view of Latin America.

NOTES

1. See http://www.panda.org/about_our_earth/ecoregions/ecoregion_list/, "Global 200—the Network of Life," for the World Wildlife Fund's 238 ecoregions of the Earth, and http://www.conservation.org for Conservation International's 34 Biodiversity Hotspots.

2. The original publication by Shreve in 1951 (Carnegie Institution of Washington, Publication 591) was reprinted as part of the *Vegetation and Flora of the Sonoran Desert* (Shreve & Wiggins, 1964). The latter date and reference are used here because that publication is more widely available. Many of the high-quality glass plates included in the original were lost and re-photographed for the later reprint (Wiggins, in Shreve & Wiggins, 1964).

3. The agaves of the North American deserts were studied by H. Gentry (1982), and his monograph has recently been reprinted by the University of Arizona Press (see References).

4. Fossils are meager for many fungi and non-reef-forming algae (other than *Botryococcus*, *Pediastrum*, and some diatoms). To encourage further study, a survey was made of the variation in fungal spores, and their survival in acetolysis as a measure of potential fossilization (Graham, 1962). In addition, several algae were cultured (*Closterium*, *Cosmarium*, *Protosiphon*) and the zygospores treated in the same manner, along with spores from 15 genera and 21 species of myxomycetes (Graham, 1971). There was variation, many did survive acteolysis, and these are now being reported in increasing numbers from the fossil record.

5. Included are other Web sites of interest; e.g., historical collections: Sloane Jamaican collections at BM (British Museum), http://www.nhm.ac.uk/research-curation/research/projects/sloane-herbarium/; botanical institutions within the Greater Antilles: Jardín Botánico Nacional República Dominicana, http://www.jbn-sdq.org/.

REFERENCES

(Including references for Appendix 1)

Abbad y Lasierra, I. 1866. Historia Geográfica, Civil y Natural de la Isla de San Juan Bautista de Puerto Rico. Imprenta y Libreria de Acosta, San Juan.

Ab'Saber, A. N. 1977. Domínios morfoclimáticos e Fitogeográficos Sulamericanos. Domínios Naturais da America do Sul ha 13,000–18,000 Anos, Primeira Approximação. Universidade de São Paulo, São Paulo. Scale ~1:15,873,000.

Adams, C. D. 1972. Flowering Plants of Jamaica. University of the West Indies, Kingston, Jamaica.

Adamoli, J. A. 1986. Fitogeografía do pantanal. Anais 1º Simpósio Recursos Naturais Sócio-econômicos do Pantanal, Embrapa-CPAP (Corumbá, Brazil, Nov./Dec., 1984). pp. 105–106.

Aide, T. M. and H. R. Grau. 2004. Globalization, migration, and Latin American ecosystems. Science 305: 1915–1916.

Alain, H. L. 1962. Flora de Cuba, Vol. V. Editorial Universitaria, Universidad de Puerto Rico, Río Piedras (supplement, 1969).

Albrecht, G. 1952–1953. The Schuss-*Yucca*. Sci. Monthly 75 (1952): 250–252, 320–321; 76 (1953): 51–53.

Allaby, A. and M. Allaby. 1999. A Dictionary of Earth Sciences. 2nd ed. Oxford University Press, Oxford, U.K.

Allen, P. H. 1956. The Rain Forests of Golfo Dulce. University of Florida Press, Gainesville.

Almeida, L., A. M. Cleef, A. Herrera, A. Velázquez, and I. Luna. 1994. El zacatonal alpino del Volcán Popocatépetl, México y su posición en las montañas tropicales de América. Phytocoenologia 22: 391–436.

Anaya, L. A., R. Hernández S., and X. Madrigal S. 1980. La vegetación y los suelos de un transecto altitudunal del declive occidental del Iztaccíhuatl (México). Bol. Técn. Inst. Nac. Invest. Forest., Mexico 65.

Anderson, A. B., I. Mousasticoshvily Jr., and D. S. Macedo. 1999. Logging of *Virola surinamensis* in the Amazon floodplain: Impacts and alternatives. *In:* C. Padoch, J. Márcio Ayres, M. Pinedo-Vasquez, and A. Henderson (eds.), Várzea: Diversity, Development, and Conservation of Amazonia's Whitewater Floodplains. New York Botanical Garden Press, Bronx. pp. 119–133.

Areces-Mallea, A., A. S. Weakley, and R. Sayre. 1999. A Guide to Caribbean Vegetation Types, Classification Systems and Descriptions. The Nature Conservancy, Arlington, VA. [See electronic addresses, Conserve Online.]

Asner, G. P. et al. (+ 5 authors). 2005. Selective logging in the Brazilian Amazon. Science 310: 480–482. ["We developed a large-scale, high-resolution, automated remote-sensing analysis of selective logging in the top five timber-producing states of the Brazilian Amazon. …Each year, 27 million to 50 million cubic meters of wood were extracted, and a gross flux of ~0.1 billion metric tons of carbon was destined for release to the atmosphere by logging."]

Asprey, G. F. and R. G. Robbins. 1953. The vegetation of Jamaica. Ecol. Monogr. 23: 359–412.

Ataroff, M. 2001. Venezuela. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 397–442.

Balslev, H. 1988. Distribution patterns of Ecuadorean plant species. Taxon 37: 567–577.

——— and J. L. Luteyn (eds.). 1992. Páramo: An Andean Ecosystem Under Human Influence. Academic Press, London.

———, ———, B. Ollgaard, and L. B. Holm-Nielsen. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. Opera Bot. 92: 37–55.

Barbour, M. G. and W. D. Billings (eds.). 2000. North American Terrestrial Vegetation. 2nd ed. Cambridge University Press, Cambridge, U.K.

Barbour, W. R. 1942. Forest types of tropical America. Caribbean Forester 3: 137–150.

Barboza M., F. R. et al. (+ 6 authors). 1999. Paraguay Regional Occidental. Mapa de Suelo. Ministerio de Agricultura y Ganadéria, Dirección Ordenamiento Ambiental. San Lorenso, Paraguay. Escala 1:750,000.

Bartlett, A. S. and E. S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change). *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 203–299.

Beaman, J. H. 1962. The timberlines of Iztaccíhuatl and Popocatépetl, Mexico. Ecology 43: 377–385.

———. 1965. A preliminary ecological study of the alpine flora of Popocatépetl and Iztaccíhuatl. Bol. Bot. Soc. Mexico 29: 63–75.

Beard, J. S. 1944. Climax vegetation in tropical America. Ecology 25: 127–158.

———. 1949. The Natural Vegetation of the Windward and Leeward Islands. Clarendon Press, Oxford, U.K.

———. 1953. The savanna vegetation of northern tropical America. Ecol. Monogr. 23: 149–215.

———. 1955. The classification of tropical American vegetation-types. Ecology 36: 89–100.

Bennett, C. F., Jr. 1963. A phytophysiognomic reconnaissance of Barro Colorado Island, Canal Zone. Smithsonian Misc. Collect. 145: 1–8.

———. 1968. Human influences on the zoogeography of Panama. Ibero-Americana 51: 1–112.

Berendsohn, W. 1991. The Arboreal Vegetation of the Laderas de la Laguna, a Neotropical Forest Fragment in El Salvador. C. A. J. Cramer, Berlin.

Bermingham, E. and C. W. Dick. 2005. Overview: The history and ecology of tropical rainforest communities. *In:* E. Bermingham, C. W. Dick, and C. Moritz (eds.), Tropical Rainforests: Past, Present, and Future. University of Chicago Press, Chicago. pp. 7–15.

———, ———, and C. Moritz (eds.). 2005. Tropical Rainforests: Past, Present, and Future. University of Chicago Press, Chicago.

Betancourt, J. L. 2004. Arid lands paleobiogeography: The rodent midden record in the Americas. *In:* M. V. Lomolino and L. R. Heaney (eds.), Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland, MA. pp. 27–46.

———, T. R. Van Devender, and P. S. Martin (eds.). 1990. Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson.

Beurton, C. 1993. Kritische Anmerkungen zur behandlung von vertretern der Gattung *Zantholylum* L. s.l. in A. Borhidi's "Phytogeography and Vegetation Ecology in Cuba." Feddes Repert. 104: 307–308.

Blydenstein, J. 1967. Tropical savanna vegetation of the llanos of Colombia. Ecology 48: 1–15.

Bolay, E. 1997. The Dominican Republic: A Country between Rain Forest and Desert. Contributions to the Ecology of a Caribbean Island. Margraf Verlag, Weikersheim, Germany.

Boom, B. M. 1990. Flora and vegetation of the Guayana-Llanos ecotone in estado Bolívar, Venezuela. Mem. N. Y. Bot. Gard. 64: 254–278.

Borhidi, A. 1996. Phytogeography and Vegetation Ecology of Cuba. Akadémiai Kiadó, Budapest.

Boros, A. and M. Járai-Komlódi. 1975. An Atlas of Recent European Moss Spores. Akadémiai Kiadó, Budapest.

Boucher, D. H. 1983. *Quercus oleoides* (roble encino, oak). *In:* D. H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago. pp. 319–320.

Bourlière, F. (ed.). 1983. Tropical Savannas. Ecosystems of the World 13. Elsevier Science Publishers, Amsterdam.

Brako, L. and J. L. Zarucchi. 1993. Catalogue of the Flowering Plants and Gymnosperms of Peru. Monogr. Syst. Bot. Missouri Bot. Gard. 45.

Breedlove, D. E. 1973. The phytogeography and vegetation of Chiapas (Mexico). *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 149–165.

———. 1981. Introduction to the flora of Chiapas. *In:* D. E. Breedlove (ed.), Flora of Chiapas, Part 1. California Academy of Sciences, San Francisco. pp. 1–35.

Bridgewater, S., A. Ibáñez, J. A. Ratter, and P. Furley. 2002. Vegetation classification and floristics of the savannas and associated wetlands of the Río Bravo Conservation and Management Area, Belize. Edinburgh J. Bot. 59: 421–442.

Britton, N. L. and P. Wilson. 1923 et seq. Botany of Porto Rico and the Virgin Islands, Descriptive Flora—Spermatophyta. Scientific Survey of Porto Rico and the Virgin Islands, Vols. V and VI. New York Academy of Sciences, New York.

Brown, A. D., H. R. Grau, L. R. Malizia, and A. Grau. 2001. Argentina. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 622–659.

Bruce, V. 2001. No Apparent Danger: The True Story of Volcanic Disaster at Galeras and Nevado del Ruiz. HarperCollins Publishers, New York.

Bubb, P. 2001. Desarrollo de una base e datos para los bosques nublados del neotrópico. *In:* M. Kappelle and A. D. Brown (eds.), Bosque Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 51–62.

Bullock, S. H., H. A. Mooney, and E. Medina (eds.). 1995. Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, U.K.

Burger, W. (ed.). 1971. Flora Costaricensis. Fieldiana, Bot. 35: 1–227.

———. 1977. Flora Costaricensis. Fieldiana, Bot. 40: 1–291.

Burnham, R. J. and K. R. Johnson. 2004. South American palaeobotany and the origin of neotropical rainforests. Philos. Trans., Ser. B 359: 1595–1610.

Cabrera, A. L. 1971. Fitogeografía de la República Argentina. Bol. Soc. Argent. Bot. 14: 1–42.

———. 1976. Regiones fitogeograficas Argentinas. Enciclopedia Argentina Agricultura y Jardineria, 2nd ed., Tomo II. Editorial Acme, Buenos Aires.

——— and E. M. Zardini. 1978. Manual de la Flora de los Alrededores de Buenos Aires. 2nd ed. Editorial Acme, Buenos Aires.

Cain, S. A. and L. G. Cain. 1944. Size-frequency studies of *Pinus palustris* pollen. Ecology 25: 229–232.

Campbell, D. G., D. C. Daly, G. T. Prance, and U. N. Maciel. 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. Brittonia 38: 369–393.

———, J. L. Stone, and A. Rosas Jr. 1992. A comparison of the phytosociology and dynamics of three floodplain (várzea) forests of known ages, Rio Juruá, western Brazilian Amazon. Bot. J. Linn. Soc. 108: 213–237.

Campos-Enriquez, J. O., J. Ortega-Ramírez, D. Alatriste-Vilchis, R. Cruz-Gática, and E. Cabral-Cano. 1999. Relationship between extensional tectonic style and the paleoclimatic elements at Laguna El Fresnal, Chihuahua Desert, Mexico. Geomorphology 28: 75–94.

Cañadas Cruz, L. 1983. El mapa bioclimático y ecológico del Ecuador. Banco Central del Ecuador, Quito.

Cano, E. B. (ed.). 2006. Biodiversidad de Guatemala. Universidad del Valle de Guatemala, Ciudad de Guatemala.

Carias, C. B. and J. A. Steyermark. 1976. Simas de Sarisariñama y su vegetación. Bol. Soc. Venez. Ci. Nat. No. 132–133: 179–405, 549–624.

Cartron, J.-L., G. Ceballos, and R. S. Felger. 2005. Biodiversity, Ecosystems, and Conservation in Northern Mexico. Oxford University Press, Oxford, U.K.

Case, T. J. and M. L. Cody (eds.). 1983. Island Biogeography in the Sea of Cortez. University of California Press, Berkeley.

Castro, A., F. R. Martins, J. Y. Tamashiro, and G. J. Shepherd.

1999. How rich is the flora of Brazilian cerrados? Ann. Missouri Bot. Gard. 86: 192–224.

Cavalcanti, T. B. and A. E. Ramos. 2001 et seq. Flora do Distrito Federal, Brasil. Vol. 1 et seq. Embrapa, Brasília, D.F.

Cavelier, J., T. M. Aide, C. Santos, A. M. Eusse, and J. M. Dupuy. 1998. The savannization of moist forests in the Sierra Nevada de Santa Marta, Colombia. J. Biogeogr. 25: 901–912.

———, D. Lizcaíno, and M. T. Pulido. 2001. Colombia. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 443–496.

Cedeño-Maldonado, J. and G. J. Breckon. 1996. Serpentine endemism in the flora of Puerto Rico. Caribbean J. Sci. 32: 348–356.

Chapman, A. D. 2005. Numbers of living species in Australia and the world. Report for the Department of the Environment and Heritage. Canberra, Australia.

Chaves, S. A. M. and O. M. Barth. 1988. Tipos polínicos encontrados em amostras de mel do Pantanal de Nhecolândia, Mato Grosso do Sul. Resumos Congresso Nacional de Botánica, Belém: 117.

——— and ———. 1989. Identificação dos tipos polínicos em amostras de mel na subregião da Nhecolândia, Corumbá, Pantanal, Mato Grosso do Sul. Resumos Congresso Nacional de Botánica, Cuiabá: 211.

Chodat, R. and W. Vischer. 1977. La Vegetation du Paraguay. Reprint, J. Cramer, Vaduz, Germany. [Reprint of articles published in various issues of the Bulletin de la Société Botanique de Genève.]

Chernoff, B. and P. W. Willink (eds.). 1999. A Biological Assessment of the Aquatic Ecosystems of the Upper Río Orthon Basin, Pando, Bolivia. Bull. Biol. Assessment 15, Conservation International, Washington, D.C.

Churchill, S. P., H. Balslev, E. Forero, and J. L. Luteyn (eds.). 1995. Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden Press, Bronx.

Ciferri, R. 1936. Studio geobotanico dell'Isola Hispaniola (Antille). Atti Ist. Bot. Univ. Pavia 8: 3–336.

Clark, H. L. and R. L. Liesner. 1989. Angiosperms. Appendix A.1. *In:* C. F. Jordan (ed.), An Amazonian Rain Forest. Man and the Biosphere Series, Vol. 2. UNESCO and The Parthenon Publishing Group, Park Ridge, NJ. pp. 111–120. [Reference in Appendix 1.27.]

Cleef, A. M. 1979. The phytogeographical position of the neotropical vascular páramo flora with special reference to the Colombian Cordillera Oriental. *In:* K. Larsen and L. Holm-Nielsen (eds.), Tropical Botany. Academic Press, London. pp. 175–184.

———. 1981. The Vegetation of the Páramos of the Colombian Cordillera Oriental. Diss. Bot. 61. J. Cramer, Vaduz, Germany. [Also printed as The Quaternary of Colombia, Vol. 9.]

——— and A. Chaverri P. 1992. Phytogeography of the páramo flora of Cordillera de Talamanca, Costa Rica. *In:* H. Balslev and J. L. Luteyn (eds.), Páramo: An Andean Ecosystem under Human Influence. Academic Press, London. pp. 45–60.

———, O. Rangel Ch., T. van der Hammen, and R. Jaramillo M. 1984. La vegetación de las selvas transecto Buritaca. Ecoandes 2: 267–406.

Colinvaux, P., P. de Oliveira, and J. Moreno-Patiño. 1999. Amazon Pollen Manual and Atlas. Harwood Academic Publishers, Amsterdam.

Colón, F. 1959. The Life of the Admiral Christopher Columbus by His Son Ferdinand (translated and annotated by B. Keen). Rutgers University Press, New Brunswick, NJ.

Condit, R. 1998. Tropical Forest Census Plots. Springer Verlag, Berlin.

Correa, M. N. 1969 et seq. Flora Patagónica de la República Argentina. Colección Cientifica del INTA (Instituto Nacional de Tecnología Agropecuaria), Buenos Aires.

Cremers, G. and M. Hoff. 1990 et seq. Inventaire Taxonomique des Plantes de La Guyane Française. Backhuys Publishers BV., Leiden, The Netherlands.

Crepet, W. L. and K. C. Nixon. 1989a. Earliest megafossil evidence of Fagaceae: Phylogenetic and biogeographic implications. Amer. J. Bot. 76: 842–855.

——— and ———. 1989b. Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. Amer. J. Bot. 76: 1493–1505.

Croat, T. B. 1978. Flora of Barro Colorado Island. Board of Trustees of the Leland Stanford Jr., Stanford University Press, Stanford, CA.

Cuatrecasas, J. 1957. A sketch of the vegetation of the north-Andean province. Proc. 8th Pacific Sci. Congr. 4: 167–173.

Dallman, P. R. 1998. Plant Life in the World's Mediterranean Climates. California Native Plant Society and University of California Press, Berkeley.

Daly, D. C. and J. D. Mitchell. 2000. Lowland vegetation of tropical South America—An overview. *In:* D. Lentz (ed.), Imperfect Balance: Landscape Transformations in the pre-Columbian Americas. Columbia University Press, New York. pp. 391–454.

——— and G. T. Prance. 1988. Brazilian Amazon. *In:* D. G. Campbell and H. D. Hammon (eds.), Floristic Inventory of Tropical Countries: The Status of Plant Systematics, Collections, and Vegetation, plus Recommendations for the Future. New York Botanical Garden Press, Bronx. pp. 402–426.

Dansereau, P. 1966. Studies on the vegetation of Puerto Rico, I. Univ. Puerto Rico Spec. Publ. No. 1: 1–45.

D'Arcy, W. G. 1987. Flora of Panama, Checklist and Index. Part I. The Introduction and Checklist. Part II. Index. Monogr. Syst. Bot. Missouri Bot. Gard. 17

——— and M. D. Correa A. (eds.). 1985. The Botany and Natural History of Panama. Monogr. Syst. Bot. Missouri Bot. Gard. 10.

Davidse, G., M. Sousa Sánchez, and S. Knapp (editores ge-

nerales). 1994 et seq. Flora Mesoamericana. Universidad Nacional Autónoma de México, México, D.F., and published in association with the Missouri Botanical Garden, St. Louis, and the Natural History Museum, London.

Davis, J. H., Jr. 1940. The ecology and geologic role of mangroves in Florida. Carnegie Inst. Wash. Publ. No. 517: 303–412.

Davis, T. A. W. and P. W. Richards. 1933–1934. The vegetation of Moraballi Creek, British Guiana: An ecological study of a limited area of tropical rain forest. Parts I, II. J. Ecol. 21: 350–384; 22: 106–155.

de Terra, H. 1955. Humboldt: The Life and Times of Alexander von Humboldt, 1769–1859. Alfred A. Knopf, New York.

Dejoux, C. and A. Iltis (eds.). 1992. Lake Titicaca: A Synthesis of Limnological Knowledge. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Delgadillo, J. 1992. Florística y Ecología del Norte de Baja California. Universidad Autónoma de Baja California, Mexicali, Mexico.

Dickson, D. 1993. Six volcanologists killed in Colombian eruption. Nature 361: 193.

Dirección de Suelos y Fertilizantes. 1976. Carta de Reconocimiento de Suelos de Uruguay y Leyenda. Ministerio de Agricultura y Pesca, Montevideo. Escala 1:1,000,000.

Dodson, C. H. and A. H. Gentry. 1978. Flora of the Río Palenque Science Center. Selbyana 4: 1–628.

———, ———, and F. M. Valverde. 1986. Flora of Jauneche Los Ríos, Ecuador. Selbyana 8: 1–512.

Dorr, L. J., B. Stergios, A. R. Smith, and N. L. Cuello A. 2000. Catalogue of the vascular plants of Guaramacal National Park, Portuguesa and Tujillo States, Venezuela. Contrib. U.S. Natl. Herb. 40: 1–155.

Dubs, B. 1994. Differentiation of woodland and wet savanna habitats in the pantanal of Mato Grosso, Brazil. The Botany of Mato Grosso, Series B. Betrona-Verlag, Küsnacht, Switzerland.

———. 1998. Prodromus Florae Matogrossensis. Betrona-Verlag, Küsnacht, Switzerland.

Ducke, A. and G. A. Black. 1953. Phytogeographical notes on the Brazilian Amazon. Anais Acad. Brasil. Ci. 25: 1–46.

——— and ———. 1954. Notas sobre a fitogeografía da Amazônia Brasileira. Bol. Técn. Inst. Agron. N. 29: 1–62.

Duivenvoorden, J. F. and A. M. Cleef. 1994. Amazonian savanna vegetation on the sandstone plateau near Araracuara, Colombia. Phytocoenologia 24: 197–232.

——— and J. M. Lips. 1995. A Land Ecological Study of Soils, Vegetation, and Plant Diversity in Colombian Amazonia. Tropenbos Series 12, The Tropenbos Foundation, Wageningen, The Netherlands. [Also reprinted in The Quaternary of Colombia, Vol. 20.]

Duke, J. A. and D. M. Porter. 1970. Darién Phytosociological Dictionary. Battelle Memorial Institute, Columbus, OH.

Dvorak, W. S., J. L. Hambrick, and E. A. Gutiérrez. 2005. The origin of Caribbean pine in the seasonal swamps of the Yucatán. Int. J. Pl. Sci. 166: 985–994.

Eggers, H. F. A. 1879. Flora of St. Croix and the Virgin Islands, West Indies. National Museum Bulletin 13, U.S. Government Printing Office, Washington, D.C.

Eiten, G. 1972. The cerrado vegetation of Brazil. Bot. Rev. 38: 201–341.

———. 1978. Delimitation of the cerrado concept. Vegetatio 36: 169–178.

———. 1982. Brazilian "savannas." *In:* B. J. Huntley and B. H. Walker (eds.), Ecology of Tropical Savannas. Ecological Studies No. 42. Springer Verlag, Berlin. pp. 25–47.

Ekman, E. K. 1928. A botanical excursion in La Hotte, Haiti. Svenska Bot. Tidskr. 22: 200–219.

Erlanson, C. O. 1946. The vegetation of San José Island, Republic of Panama. Smithsonian Misc. Coll. 106: 1–12.

Erwin, T. L. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. Coleopterist Bull. 36: 74–82.

Espejo-Serna, A., A. R. López-Ferrari, and I. Salgado Ugarte. 2004. A current estimate of angiosperm diversity in Mexico. Taxon 53: 127–130.

Espinal, T. L. S. and M. E. Montenegro. 1963. Formaciones Vegetales de Colombia. Memoria Explicativa sobre el Mapa Ecológico. Instituto Geográfico "Agustín Codazzi," Bogotá.

Etter, A. 1998. Mapa General de Ecosistemas de Colombia. Instituto Investigación Recursos Biologicos Alexander von Humboldt, Bogotá. Escala 1:2,000,000.

Ewel, J. J., A. Madriz, and J. A. Tosi Jr. 1976. Zonas de la vida de Venezuela. Ministerio de Agricultura y Cria, Fondo Nacional de Investigaciones Agropecuarias, Caracas. Text and map, Escala 1:2,000,000.

——— and J. L. Whitmore. 1973. The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands. U.S. Forest Service Research Paper 18. Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Faber-Landendoen, D. and A. H. Gentry. 1991. The structure and diversity of rain forests at Bajo Calima, Chocó region, western Colombia. Biotropica 23: 2–11.

Fanshawe, D. 1952. The Vegetation of British Guiana: A Preliminary Review. Inst. Paper 29, Commonwealth Forestry Institute, Oxford, U.K.

Figueroa Colón, J. (ed.). 1996. The scientific survey of Puerto Rico and the Virgin Islands, an eighty-year reassessment of the island's natural history. Ann. N. Y. Acad. Sci. 77: 1–273.

Filgueiras, T. S. 2002. Herbaceous plant communities. *In:* P. S. Oliveira and R. J. Marquis (eds.), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. pp. 121–139.

——— and B. A. S. Pereira. 1994. Flora do Distrito Federal. *In:* M. Novaes Pinto (ed.), Cerrado: Caracterização, Ocupação e Perspectivas. 2nd ed. Editoria Universidade de Brasília, Brasília. pp. 345-404.

Fittkau, E. J., J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli

(eds.). 1969. Biogeography and Ecology in South America, 2 Vols. Dr. W. Junk Publishers, The Hague.

Flora of North America Editorial Committee (eds.). 1993 et seq. Flora of North America North of Mexico. Oxford University Press, Oxford, U.K.

Flores M., G., J. Jiménez L., X. Madrigal S., F. Moncayo R., and F. Takaki T. 1971. Memoria del Mapa de Tipos de Vegetación de la República Mexicana. Secretaría de Recursos Hidráulicos, Mexico, D.F. 59 pp.

Freire-Fierro, A. 2004. Botánica Sistemática Ecuadoriana. Missouri Botanical Garden Press, St. Louis.

Furley, P. A. 1999. The nature and diversity of neotropical savanna vegetation with particular reference to the Brazilian cerrados. Global Ecol. Biogeogr. 8: 223–241.

Gajardo, R. 1994. La Vegetación Natural de Chile, Classificación y Distribución Geográfica. Editorial Universitaria, Santiago.

Galindo-Leal, C. and I. de Gusmão-Câmara (eds.). 2003. The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook. Island Press, Washington, D.C.

Garver, R. D. 1947. Republic of Panama Report. Office of Foreign Agricultural Relations, Washington, D.C.

Geisler, F. 1945. A study of pollen grains of thirty-two species of grasses. Butler Univ. Bot. Studies 7: 1–9.

Gentry, A. H. 1982. Patterns of neotropical plant species diversity. *In:* W. Hecht, B. Wallace, and G. T. Prance (eds.), Evolutionary Biology, Vol. 15. Plenum Publishing, New York. pp. 1–84.

———. 1986. Species richness and floristic composition of Chocó region plant communities. Caldasia 15: 71–91.

——— (ed.). 1990. Four Neotropical Rainforests. Yale University Press, New Haven, CT.

———. 1993. A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru) with Supplementary Notes on Herbaceous Taxa. Conservation International, Washington, D.C.

———. 1995. Diversity and floristic composition of neotropical dry forests. *In:* S. H. Bullock, H. A. Mooney, and E. Medina (eds.), Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, U.K. pp. 146–194.

——— and C. Dodson. 1987. Contributions of nontrees to species richness of a tropical forest. Biotropica 19: 149–156.

——— and J. Terborgh. 1990. Composition and dynamics of the Cocha Cashu "mature" floodplain forest. *In:* A. H. Gentry (ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT. pp. 542–564.

Gentry, H. S. 1942. Río Mayo plants, a study of the flora and vegetation of the Valley of the Río Mayo, Sonora. Carnegie Inst. Wash. Publ. 527: 1–328. [Revised and edited by P. S. Martin, D. Yetman, et al., 1999, University of Arizona Press, Tucson.]

———. 1982. Agaves of Continental North America. University of Arizona Press, Tucson. [Reprinted, University of Arizona Press.]

Gleason, H. A. and M. T. Cook. 1926. Plant Ecology of Porto Rico. Scientific Survey of Porto Rico and the Virgin Islands, Vol. VII, Pts. 1 and 2. New York Academy of Sciences, New York.

Goldman, E. A. 1920. Mammals of Panama. Smithsonian Misc. Collect. 69: 1–309.

——— and J. B. Zetek. 1926. Panama. *In:* V. E. Shelford (ed.), Naturalist's Guide to the Americas. Williams and Wilkins, Baltimore. pp. 612–622.

Golley, F. B., J. T. McGinnis, R. G. Clements, G. I. Child, and M. J. Duever. 1969. The structure of tropical forests in Panama and Colombia. BioScience 19: 693–696.

Gómez, L. D. and J. M. Savage. 1983. Searchers on that rich coast: Costa Rican field biology, 1400–1980. *In:* D. H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago. pp. 1–11.

Gómez-Laurito, J. and L. D. Gómez. 1989. *Ticodendron*: A new tree from Central America. Ann. Missouri Bot. Gard. 76: 1148–1151.

——— and ———. 1991. Ticodendraceae: A new family of flowering plants. Ann. Missouri Bot. Gard. 78: 87–88.

Gómez-Pompa, A. 1965. La vegetación de México. Bol. Soc. Bot. Méx. 29: 76–120.

———. 1973. Ecology of the vegetation of Veracruz. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 73–148.

González Soriano, E., R. Dirzo, and R. C. Vogt (eds.). 1997. Historia Natural de Los Tuxtlas. Universidad Nacional Autónoma de México, México, D.F.

Goodland, R. A. 1970. Plants of the cerrado vegetation of Brazil. Phytologia 20: 57–78.

———. 1971. A physiognomic analysis of the "cerrado" vegetation of central Brazil. J. Ecol. 59: 411–419.

——— and M. G. Ferri. 1979. Ecología do Cerrado. Livraria Itatiaia Editora, Belo Horizonte; Editora da Universidade de São Paulo, São Paulo.

Gordon, A. G. 1968. Ecology of *Picea chihuahuana* Martinez. Ecology 49: 880–896.

Gottsberger, G. and I. Silberdauer-Gottsberger. 2006. Life in the Cerrado: A South American Tropical Seasonal Ecosystem. Vol. 1. Origin, Structure, Dynamics and Plant Use. Vol. 2. Pollination and Seed Dispersal. Reta Verlag, Ulm, Germany.

Gouvêa, J. B. S., L. A. Silva, and M. Hori. 1976. 1. Fitografía. *In:* Diagnóstico Socioeconômico da Região Cacaueira, Recursos Florestais, Vol. 7. Comissão Executiva do Plano da Lavoura Cacaueira y Instituto Interamericano de Ciências Agrícolas–OEA, Ilhéus, Bahia, Brazil.

Govaerts, R. 2001. How many species of seed plants are there? Taxon 50: 1085–1090.

Gradstein, S. R. and J.-P. Frahm. 1987. Die floristiche Höhengieiderung der Moose entland des BRYOTROP-transektes in NO–Peru. Nova Hedwigia 88: 105–113.

Graham, A. 1962. The role of fungal spores in palynology. J. Paleontol. 36: 60–68.

———. 1971. The role of myxomycete spores in palynology (with a brief note on the morphology of certain algal zygospores). Rev. Palaeobot. Palynol. 11: 89–99.

———. 1999. Studies in Neotropical Paleobotany. XIII. An Oligo–Miocene palynoflora from Simojovel (Chiapas, Mexico). Amer. J. Bot. 86: 17–31. [Reference in Appendix 1.2.]

Granville, J.-J. de. 1988. Phytogeographical characteristics of the Guianan forests. Taxon 37: 578–594.

———. 2002. Milieux et formations végétales de Guyane. Acta Bot. Gallica 149: 319–337.

Grayum, M. H., B. E. Hammel, S. Troyo, and N. Zamora. 2004. Historia/History. *In:* B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora (eds.), Manual de Plantas de Costa Rica. Vol. 1. Monogr. Syst. Bot. Missouri Bot. Gard. 97: 1–50.

Grubb, P. J. 1974. Factors controlling the distribution of forest-types on tropical mountains: New facts and a new perspective. *In:* J. R. Flenley (ed.), Altitudinal Zonation in Malesia. University of Hull, Department of Geography, Hull, U.K. pp. 13–46.

———, J. R. Lloyd, T. D. Pennington, and T. C. Whitmore. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. J. Ecol. 51: 567–601.

Guarim, V., E. Moraes, G. T. Prance, and J. A. Ratter. 2000. Inventory of a mesotrophic *Callisthene* cerradão in the pantanal of Mato Grosso, Brazil. Edinburgh J. Bot. 57: 429–436.

Haack, H. 1985. Sudamerika, Klima und Vegetation. Geographisch-Kartographische Anstalt, Gotha, Germany. Scale 1:6,000,000.

Haase, R. and S. G. Beck. 1989. Structure and composition of savanna vegetation in northern Bolivia: A preliminary report. Brittonia 41: 80–100.

Haber, W. A. 2000. Plants and vegetation. *In:* N. M. Nadkarni and N. T. Wheelwright (eds.), Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, Oxford, U.K. pp. 39–94.

———, W. Zuchowski, and E. Bello. 1996. An Introduction to Cloud Forest Trees: Monteverde, Costa Rica. Copyright by the author (W. A. Haber).

Hamilton, L. S., J. O. Juvik, and F. N. Scatena (eds.). 1995. Tropical Montane Cloud Forests. Springer Verlag, Berlin.

Hammel, B. E., M. H. Grayum, C. Herrera, and N. Zamora (eds.). 2003 et seq. Manual de Plantas de Costa Rica. Monogr. Syst. Bot. Missouri Bot. Gard. 92, 93, 97, 111.

——— and W. G. Burger. 1991. Neither oak nor alder, but nearly: The history of Ticodendraceae. Ann. Missouri Bot. Gard. 78: 89–95.

Hammond, P. M. 1995. The current magnitude of biodiversity. *In:* V. H. Heywood (ed.), Global Biodiversity Assessment. Cambridge University Press, Cambridge, U.K. pp. 113–138.

Harley, R. M. and N. A. Simmons. 1986. Florula of Mucugê. Royal Botanic Gardens, Kew, Richmond, U.K.

Harling, G. 1979. The vegetation types of Ecuador—A brief survey. *In:* K. Larsen and L. B. Holm-Nielsen (eds.), Tropical Botany. Academic Press, London. pp. 165–174.

——— and B. Sparre. 1973 et seq. Flora of Ecuador. Vol. 1 et seq. Department of Systematic Botany, University of Göteborg and Section for Botany, Riksmuseum, Stockholm.

Hartshorn, G. S. 1983. Plants. *In:* D. H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago. pp. 118–183.

———. 2000. Tropical and subtropical vegetation of Mesoamerica. *In:* M. G. Barbour and W. D. Billings (eds.), North American Terrestrial Vegetation. 2nd ed. Cambridge University Press, Cambridge, U.K. pp. 623–659.

——— and R. Peralta. 1988. Preliminary description of primary forests along the La Selva–Volcán Barva altitudinal transect, Costa Rica. *In:* F. Almeda and C. M. Pringle (eds.), Tropical Rainforests: Diversity and Conservation. California Academy of Sciences, San Francisco. pp. 281–295.

Hauman, L. 1984. Los generos de fanerogamas de Argentina, claves para su identificación. Bol. Soc. Argent. Bot. 23: 1–384.

Heckman, C. W. 1998. The Pantanal of Poconé: Biota and Ecology in the Northern Section of the World's Largest Pristine Wetland. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Helmer, E. H., O. Ramos, T. M. López, M. Quiñones, and W. Diaz. 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. Caribbean J. Sci. 38: 165–183.

Henrickson, J. 1972. A taxonomic revision of the Fouquieriaceae. Aliso 7: 439–537.

———. 1973. Fouquieriaceae DC. *In:* S. Nilsson (ed.), World Pollen and Spore Flora 1. Almqvist & Wiksell, Stockholm. pp. 1–12.

——— and M. C. Johnston. 1986. Vegetation and community types of the Chihuahuan Desert. *In:* J. C. Barlow, A. M. Powell, and B. N. Timmermann (eds.), Chihuahuan Desert—U.S. and Mexico, Vol. 11. Chihuahuan Desert Research Institute, Sul Ross State University, Alpine, TX. pp. 20–39.

——— and R. M. Straw. 1976. A Gazetteer of the Chihuahuan Desert Region, A Supplement to the Chihuahuan Desert Flora. California State University, Los Angeles.

Hernandez-C., J., G. Lozano-C., and J. E. Henao-S. 1980. Finding the genus *Trigonobalanus* Fagaceae in the neotropics 2. Caldasia 13: 9–44.

Heusser, C. J. 1971. Pollen and Spores of Chile, Modern Types of the Pteridophyta, Gymnospermae, and Angiospermae. University of Arizona Press, Tucson.

Heyligers, P. C. 1963. Vegetation and soil of a white-sand savanna in Suriname. The Vegetation of Suriname, Vol. III. Noord-Hollandsche Uitg. Mij., Amsterdam.

Hill, R. T. 1899. Notes on the forest conditions of Porto Rico. U.S.D.A. Div. Forest. Bull. 25.

Hoehne, F. C. 1923. Phytophysionomia do estado de Mato Grosso. Compania Melhoramentos, São Paulo, Brazil, 1923: 53–58.

———. 1936. O grande Pantanal de Mato Grosso. Bol. Agric., São Paulo, pp. 443–447.

Hofmann, C.-C. 2002. Pollen distribution in sub-Recent sedimentary environments of the Orinoco Delta (Venezuela)—An actuo-palaeobotanical study. Rev. Palaeobot. Palynol. 119: 191–217.

Hogarth, P. J. 1999. The Biology of Mangroves. Oxford University Press, Oxford, U.K.

Holdridge, L. R. 1942. The pine forests of Haiti. Caribbean Forester 4: 16–22.

———. 1947a. Determination of world plant formations from simple climatic data. Science 105: 367–368.

———. 1947b. The pine forest and adjacent mountain vegetation of Haiti considered from the standpoint of a new climatic classification of plant formations. Ph.D. dissertation, University of Michigan, Ann Arbor.

———. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.

———. 1970. A system for representing structure in tropical forest associations. *In:* H. T. Odum (ed.), A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico. Division of Technical Information, U.S. Atomic Energy Commission, Washington, D.C. pp. B147–B150.

——— and G. Budowski. 1956. Report of an ecological survey of the Republic of Panama. Caribbean Forester 17: 92–110.

——— and ———. 1959. Mapa Ecológico de Panamá. Instituto Inter-Americano Ciencias Agricolas, Turrialba, Costa Rica.

———, W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi Jr. 1971. Forest Environments in Tropical Life Zones, a Pilot Study. Pergamon Press, New York.

Howard, R. A. 1968. The ecology of an elfin forest in Puerto Rico, I. Introduction and composition studies. J. Arnold Arb. 49: 381–418.

———. 1973. The vegetation of the Antilles. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 1–38.

———. 1974 et seq. Flora of the Lesser Antilles, Leeward and Windward Islands. Vol. 1, Orchidaceae. Arnold Arboretum, Jamaica Plain, MA.

——— and W. Briggs. 1953. The vegetation on coastal dog-tooth limestone in southern Cuba. J. Arnold Arb. 34: 88–94.

——— and G. R. Proctor. 1957a. Vegetation on bauxite soils in Jamaica, I. J. Arnold Arb. 38: 1–41.

——— and G. R. Proctor. 1957b. Vegetation on bauxite soils in Jamaica, II. J. Arnold Arb. 38: 151–169.

Hubbell, S. P. and R. B. Foster. 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. *In:* A. H. Gentry (ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT. pp. 522–541.

Huber, O. (ed.). 1992. El Macizo del Chimantá, Escudo de Guayana Venezuela, un Ensayo Ecológico Tepuyano. Oscar Todtmann Editores, Caracas.

———. 1995. Vegetation. *In:* J. A. Steyermark, P. E. Berry, and B. K. Holst (eds.), Flora of the Venezuelan Guayana. Vol. 1, Introduction. Missouri Botanical Garden, St. Louis; Timber Press, Portland. pp. 97–160.

——— and C. Alarcón. 1988. Vegetation Map of Venezuela. MARNR and The Nature Conservancy, Caracas. Scale 1:2,000,000.

Hueck, K. and P. Seibert. 1972. Vegetationskarte von Südamerika. Vegetations-monographien der Einzelnen Grossräume Bd. IIa. Scale 1:8,000,000.

Hughes, C. and R. Eastwood. 2006. Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. Proc. Natl. Acad. Sci. U.S.A. 103: 10334–10339.

Humboldt, A. von. 1807. Essai sur la géographie des plantes—accompagné d'un tableau physique des regions équinoxiales, fondé sur des measures executes, depuis le dixième degree de latitude boréale jusqu'au dixième degréme degree de latitude australe, pendant les années 1799, 1800, 1801, 1802 et 1803. Levrault et Schoell, Paris, France. [See also, Ideen zu einer Geographie der Pflanzen. Ed. Reprint 1963. Wissenschaftlichen Buchgesellschaft, Darmstadt, Germany.]

Humphrey, R. R. 1935. A study of *Idria columnaris* and *Fouquieria splendens*. Amer. J. Bot. 22: 184–207.

———. 1974. The Boojum and Its Home. University of Arizona Press, Tucson.

Hutchings, P. H. and P. Saenger. 1987. Ecology of Mangroves. University of Queensland Press, St. Lucia, Australia.

Huntley, B. J. and B. H. Walker (eds.). 1982. Ecology of Tropical Savannas. Ecological Studies 42. Springer Verlag, Berlin.

IBGE (Instituto Brasileiro de Geografía e Estatística). 1993. Mapa de Vegetação do Brasil. Fundação IBGE, Rio de Janeiro. Escala 1:5,000,000.

Ickert-Bond, S. M. 2002. *Ephedra* L. (Ephedraceae) in Ecuador, contributions from taxonomy, micromorphology and anatomy. *In:* A. Freire-Fierro and D. A. Neill (eds.), La Botánica en el Nuevo Milenio: Memorias del Tercer Congresso Ecuatoriano de Botánica. FUNBOTANICA, Quito. pp. 1–19.

Irion, G., W. J. Junk, and J. A. S. N. de Mello. 1997. The large central Amazonian river floodplains near Manaus: Geo-

logical, climatological, hydrological and geomorphological aspects. *In:* W. J. Junk (ed.), The Central Amazon Floodplain: Ecology of a Pulsing System. Springer Verlag, Berlin. pp. 23–46.

Islebe, G. A. 1996. Vegetation, Phytogeography, and Paleoecology of the Last 20,000 Years of Montane Central America. Ph.D. dissertation, University of Amsterdam, Amsterdam.

——— and H. Hooghiemstra. 1995. Recent pollen spectra of highland Guatemala. J. Biogeogr. 22: 1091–1099.

——— and M. Kappelle. 1994. A phytogeographical comparison between subalpine forests of Guatemala and Costa Rica. Feddes Repert. 105: 73–87.

———and A. Velázquez. 1994. Affinity among mountain ranges in megamexico: A phytogeographical scenario. Vegetatio 115: 1–9.

——— and M. E. Vélez Pérez. 2001. Guatemala. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 231–241.

Janzen, D. H. (ed.). 1983. Costa Rican Natural History. University of Chicago Press, Chicago.

Jardim, M. A. G. and I. C. Guimarães Vieira. 2001. Composicão floristica e estructura de uma floresta de várzea do estuário Amazônica, Ihla do Combu, estado do Pará, Brasil. Bol. Mus. Paraense Emilio Goeldi, Ser. Bot., 17: 333–354.

Jarzen, D. M. 1979. Spore morphology of some Anthrocerotaceae and the occurrence of *Phaeoceros* spores in the Cretaceous of North America. Pollen & Spores 21: 211–232.

Johnston, I. M. 1949. The botany of San José Island. Sargentia 8: 1–306.

Jones, G. D., V. M. Bryant Jr., M. H. Lieux, S. D. Jones, and P. D. Lingren. 1995. Pollen of the Southeastern United States: With Emphasis on Melissopalynology and Entomopalynology. American Association of Stratigraphic Palynologists, Dallas.

Jordan, C. F. (ed.). 1989. An Amazonian Rain Forest. Man and the Biosphere Series, Vol. 2. UNESCO, Paris; The Parthenon Publishing Group, Park Ridge, NJ. [Reference in Appendix 1.27.]

Jørgensen, P. M. and S. León-Yánez (eds.). 1999. Catalogue of the Vascular Plants of Ecuador. Monogr. Syst. Bot. Missouri Bot. Gard. 75.

———, M. J. Maci, T. J. Killeen, and S. G. Beck (eds.). 2005. Estudios Botánicos de la Región de Madidi. Missouri Botanical Garden Press, St. Louis.

——— and C. Ulloa Ulloa. 1994. Seed plants of the High Andes of Ecuador—A checklist. AAU Rep. 34: 1–443.

Judd, W. S. 1987. Floristic study of Morne La Visite and Pic Macaya national parks, Haiti. Bull. Florida State Mus., Biol. Sci. 32: 1–136.

Junk, W. J. (ed.). 1997. The Central Amazon Floodplain: Ecology of a Pulsing System. Springer Verlag, Berlin.

——— and C. J. da Silva. 1995. Neotropical floodplains: A comparison between the pantanal of Mato Grosso and the large Amazonian river floodplains. *In:* J. G. Tundisi, E. M. Bicudo, and T. M. Tundisi (eds.), Limnology in Brazil. Brazilian Academy of Sciences and Brazilian Limnological Society, Rio de Janeiro. pp. 195–218.

———, J. J. Ohly, M. T. F. Piedade, and M. G. M. Soares. 2000. The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management. Backhuys Publishers, Leiden.

——— and M. T. Piedade. 1997. Plant life in the floodplain with special reference to herbaceous plants. *In:* W. Junk (ed.), The Central Amazon Floodplain: Ecology of a Pulsing System. Springer Verlag, Berlin. pp. 147–185.

Kahn, F. and A. Henderson. 1999. An overview of the palms in the várzea in the Amazon region. *In:* C. Padoch, J. Márcio Ayres, M. Pinedo-Vasquez, and A. Henderson (eds.), Várzea: Diversity, Development, and Conservation of Amazonia's Whitewater Floodplains. New York Botanical Garden Press, Bronx. pp. 187–193.

Kalin Arroyo, M. T., P. H. Zedler, and M. D. Fox (eds.). 1995. Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Ecological Studies 108. Springer Verlag, Berlin.

Kappelle, M. 1995. Ecology of Mature and Recovering Talamancan Montane *Quercus* Forests, Costa Rica. Ph.D. dissertation, University of Amsterdam, Amsterdam.

———. 1996. Los Bosques de Roble (*Quercus*) de la Cordillera de Talamanca, Costa Rica. University of Amsterdam, Amsterdam; INBio, Santo Domingo de Heredia, Costa Rica.

——— and A. D. Brown (eds.). 2001. Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica.

——— and S. P. Horn (eds.). 2005. Páramos de Costa Rica. INBio, Santo Domingo de Heredia, Costa Rica.

Karez, C., C. Daniele, and L. Rodriguez Bayona. 1998. Las reservas de biósfera y el rol de la investigación científico. Ecologia 1: 10–15.

Keller, R. 1996. Identification of Tropical Woody Plants in the Absence of Flowers and Fruits: A Field Guide. Birkhäuser Verlag, Basel.

Kessler, M. 2002. The elevational gradient of Andean plant endemism: Varying influences of taxon-specific traits and topography at different taxonomic levels. J. Biogeogr. 29: 1159–1165.

——— and S. G. Beck. 2001. Bolivia. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 581–622.

Killeen, T. J., E. García E., and S. G. Beck (eds.). 1993. Guía de Arboles de Bolivia. Herbario Nacional de Bolivia, La Paz; Missouri Botanical Garden, St. Louis.

Köppen, W. 1918. Klassification der Klimate nach Temperatur, Niederschlag und Jahreslauf. Petermanns Geogr. Mitt. 64: 193–203.

———. 1936. Das geographische System der Klimate. *In:* W. Köppen and R. Geiger (eds.), Handbuch der Klimatologie, Vol. 1, Part C. Gebrüder Bornträger, Berlin.

Krajick, K. 2004. All downhill from here? Science 303: 1600–1602.

Kuhlmann, E. 1977. Vegetacão. *In:* IBGE Geographía do Brazil. Região North. IBGE, Rio de Janeiro. [Text to accompany the Instituto Brasileiro de Geografía e Estatística's vegetation map of northern Brazil.]

Laegaard, S. 1992. Influence of fire in the grass páramo vegetation of Ecuador. *In:* H. Balslev and J. L. Luteyn (eds.), Páramo: An Andean Ecosystem Under Human Influence. Academic Press, London. pp. 151–170.

Lamb, F. B. 1953. The forests of Darién, Panama. Caribbean Forester 14: 128–135.

Lauer, W. 1986. Die vegetationszonierung der Neotropics und ihr wander seit der Eiszeit. Ber. Deutsch. Bot. Ges. 99: 211–237.

———. 1989. Climate and weather. *In:* H. Leith and J. A. Werger (eds.), Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies. Ecosystems of the World 14B. Elsevier Science Publishers, Amsterdam. pp. 7–52.

———, M. D. Rafiqpoor, and I. Theisen. 2001. Physiogeographie, Vegetation und Syntaxonomie der Flora des Páramo de Papallacta (Ostkordillere Ecuador). Franz Steiner Verlag, Stuttgart.

Ledig, F. T. et al. (+ 5 authors). 2000. Locations of endangered spruce populations in Mexico and the demography of *Picea chihuahuana*. Madroño 47: 71–88.

———, P. D. Hodgskiss, K. V. Krutovski, D. B. Neale, and T. Eguiluz-Pieda. 2004. Relationships among the spruces (*Picea*, Pinaceae) of southwestern North America. Syst. Bot. 29: 275–295.

Leigh, E. G., Jr. 1999. Tropical Forest Ecology: A View from Barro Colorado Island. Oxford University Press, Oxford, U.K.

———, A. S. Rand, and D. M. Windsor (eds.). 1996. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. 2nd ed. Smithsonian Institution Press, Washington, D.C.

León, H. S. 1946. Flora de Cuba. Vol. 1. Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle," No. 8.

——— and H. Alain (Dr. E. E. Liogier). 1951–1957. Flora de Cuba. Editorial Universitaria, Universidad de Puerto Rico, Río Piedras.

Leopold, A. S. 1950. Vegetation zones of Mexico. Ecology 31: 507–518.

Leyden, B. W. 1987. Man and climate in the Maya Lowlands. Quatern. Res. 28: 407–414.

Lia, V. V., V. A. Confalonieri, C. I. Comas, and J. H. Hunziker. 2001. Molecular phylogeny of *Larrea* and its allies (Zygophyllaceae): Reticulate evolution and the probable time of creosote bush arrival to North America. Molec. Phylogen. Evol. 21: 309–320.

Lindeman, J. C. 1953. The Vegetation of the Coastal Region of Suriname. Kemink, Utrecht.

Liogier, A. H. 1985, 1988. Descriptive Flora of Puerto Rico and Adjacent Islands. Vols. 1, 2. Editorial Universitaria, Universidad de Puerto Rico, Río Piedras.

——— and L. F. Martorell. 1982. Flora of Puerto Rico and Adjacent Islands: A Systematic Synopsis. Editorial Universitaria, Universidad de Puerto Rico, Río Piedras.

Little, E. L., Jr. and F. H. Wadsworth. 1964. Common Trees of Puerto Rico and the Virgin Islands. U.S.D.A. Forest Service, Agricultural Handbook No. 249, Washington, D.C.

———, R. O. Woodbury, and F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands. 2nd ed. U.S.D.A. Forest Service, Agricultural Handbook No. 44, Washington, D.C.

Lombardo, A. 1964. Flora Arbórea y Arborescente de Uruguay. 2nd ed. Concejo Departmental de Montevideo, Montevideo.

López G., O. et al. (+ 6 authors). 1995a. República del Paraguay, Mapa de Reconocimiento de Suelos de la Region Oriental. Ministerio de Agricultura y Ganadéria, Asunción. [Imágenes Landsat, Bandas 3, 7, y 4 falso color (1991, 1992).] Escala 1:500,000.

——— et al. (+ 6 authors). 1995b. República del Paraguay, Mapa de Ordinamiento Territorial de la Region Oriental. Ministerio de Agricultura y Ganadéria, Asunción. [Imágenes Landsat, Bandas 3, 7, y 4, falso color (1991, 1992).] Escala 1:500,000.

López-Portillo, J. and E. Ezcurra. 1989. Zonation in mangrove and salt marsh vegetation at Laguna de Mecoacán, Mexico. Biotropica 21: 107–114.

Lorenzi, H. 1992. Árvores Brasilieiras, Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil. Editora Plantarum, Nova Odessa, Brazil.

Lovejoy, T. E. and R. O. Bierregaard Jr. 1990. Central Amazonian forests and the Minimum Critical Size Ecosystems Project. *In:* A. H. Gentry (ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT. pp. 60–71.

Lozano-C., G., J. Hernandez-C., and J. E. Henao-S. 1979. Finding of the genus *Trigonobalanus* Fagaceae in the neotropics 1. Caldasia 12: 517–538.

Lozano-García, M. 1984. Interpretaciones sobre la lluvia de polen en la región de San Luis Potosí, México. Bol. Soc. Bot. Méx. 46: 53–74.

——— and E. Martínez-Hernández. 1990. Palinología de Los Tuxtlas: Especies Arboreas. Universidad Nacional Autónoma de México, Instituto de Biología, Publicaciones Especiales 3. México, D.F.

Ludlow-Wiechers, B. et al. (eds.). 1991 et seq. Flora Palinológica de Guerrero. Gestión de Ecosistemas, A.C., Facultad de Ciencias, UNAM, México, D.F.

Luna Vega, I., A. Velázquez, and E. Velázquez. 2001. Mexico. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 183–229.

——— and J. Llorente Bousquets (eds.). 1993. Historia Natural del Parque Ecológico Estatal Omiltemi, Chilpancingo, Guerrero, Mexico. Universidad Nacional Autónoma de

México, México, D.F.
Lundell, C. L. 1937. The Vegetation of Petén. Publication 478, Carnegie Institution of Washington Press, Washington, D.C.
Luteyn, J. L. 1992. Páramos: Why study them? *In:* H. Balslev and J. L. Luteyn (eds.), Páramo: An Andean Ecosystem Under Human Influence. Academic Press, London. pp. 1–14.
———. 1999. Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature. New York Botanical Garden Press, Bronx.
———, A. M. Cleef, and O. Rangel Ch. 1992. Plant diversity in páramo: Towards a checklist of páramo plants and a generic flora. *In:* H. Balslev and J. L. Luteyn (eds.), Páramo: An Andean Ecosystem Under Human Influence. Academic Press, London. pp. 71–84.
Macbride, J. F. (ed.). 1936 et seq. Flora of Peru. Field Museum of Natural History, Chicago.
MacMahon, J. A. 2000. Warm deserts. *In:* M. G. Barbour and W. D. Billings (eds.), North American Terrestrial Vegetation. 2nd ed. Cambridge University Press, Cambridge, U.K. pp. 285–322.
Madison, M. 1977. Vascular epiphytes: Their systematic occurrence and salient features. Selbyana 2: 1–13.
Maguire, B. 1970. On the flora of the Guayana Highland. Biotropica 2: 85–100.
———. 1979. Guayana, region of the Roraima Sandstone Formation. *In:* K. Larsen and L. B. Holm-Nielsen (eds.), Tropical Botany. Academic Press, London. pp. 223–238.
———, R. S. Cowan, and J. J. Wurdack (and collaborators). 1953 et seq. The botany of the Guyana Highland. Mem. New York Bot. Gard. 8: 87–160.
Manchester, S. R., V. Wilde, and M. E. Collinson. 2007. Fossil cashew nuts from the Eocene of Europe: Biogeographic links between Africa and South America. Int. J. Pl. Sci. 168: 1199–1206.
Marie-Victorín, F. and H. S. León. 1942. Itineraires botanique dans l'Ile de Cuba. Contr. Inst. Bot. Univ. Montreal 41: 496 pp.
——— and ———. 1944. Itineraires botanique dans l'Ile de Cuba. Contr. Inst. Bot. Univ. Montreal 50: 410 pp.
——— and ———. 1956. Itineraires botanique dans l'Ile de Cuba. Contr. Inst. Bot. Univ. Montreal 68: 227 pp.
Marticorena, C. and M. Quezada. 1985. Catálogo de la flora vascular de Chile. Gayana Bot. 42: 1–157.
——— and R. Rodríguez (eds.). 1995 et seq. Flora de Chile. Universidad de Concepción, Concepción.
Martin, P. S. 1955. Zonal distribution of vertebrates in a Mexican cloud forest. Amer. Naturalist 89: 347–361.
———. 1958. A biogeography of reptiles and amphibians in the Gómez Farías region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool. Univ. Michigan 101: 1–102.
——— and B. E. Harrell. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology 38: 468–480.
Martínez Carretero, E. 2000. Vegetación de los Andes Centrales de la Argentina El Valle de Uspallata, Mendoza. Bol. Soc. Argent. Bot. 34: 127–148.
Martínez-Hernández, E. (+ 7 authors). 1993. Atlas de las Plantas y el Polen Utilizados por las Cinco Especies Principales de Abejas Productoras de Miel en la Región del Tacana, Chiapas, México. Universidad Nacional Autónoma de México, Instituto de Geología, México, D.F.
Martius, K. F. P. von. 1840–1906. Flora Brasiliensis. 15 Vols. R. Oldenbourg, Munich.
Materri, C. M. 1988. Restos de *Didymodon* sp. (Pottiaceae, Musci) en sedimentos Cuaternarios de Isla Gable, Argentina. Bol. Asoc. Latinoamer. Paleobot. Palin. 11: 23–27.
Matlock, R. B., Jr. and G. S. Hartshorn. 1999. Focus on field stations: La Selva Biological Station, Costa Rica. Bull. Ecol. Soc. Amer. 80: 188–193.
May, R. M. 1997. The dimensions of life on earth. *In:* P. H. Raven (ed.), Nature and Human Society: The Quest for a Sustainable World. National Academy Press, Washington, D.C. pp. 30–45.
McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.). 1994. La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago.
McEwan, C., L. A. Borrero, and A. Prieto (eds.). 1997. Patagonia: Natural History, Prehistory and Ethnography at the Uttermost End of the Earth. Princeton University Press, Princeton, NJ.
Medellín-Leal, F. 1982. The Chihuahuan Desert. *In:* G. L. Bender (ed.), Reference Handbook on the Deserts of North America, Vol. 6. Greenwood Press, Westport, CT. pp. 321–381.
Medina, E. and J. F. Silva. 1990. Savannas of northern South America: A steady state regulated by water-fire interactions on a background of low nutrient availability. J. Biogeogr. 17: 403–413.
Melgarejo, J. 1914. Memoria y descripción de la Isla de San Juan de Puerto Rico en el año 1582. Bol. Hist. Puerto Rico 1: 75–91.
Meza, P. E., G. O. de Jara, and P. R. Florentín. 1995. República del Paraguay, Mapa de Uso Actual de la Tierra de la Región Oriental (1992). Ministerio de Agricultura y Ganadéria, Dirección Ordenamiento Ambiental, San Lorenzo, Paraguay. Escala 1:500,000.
Michalowsky, M. 1953. Arboles y Arbustos del Paraguay. Ministerio de Agricultura y Ganaderia, Asunción, Paraguay.
Mihotek, K. (ed.). 1996. Comunidades Territorios Indígenas y Biodiversidad en Bolivia. Centro de Investigación y Manejo de Recursos Naturales Renovables, Santa Cruz, Bolivia.
Miranda, F. 1952–1953. La Vegetación de Chiapas. 2 vols. Ediciones del Gobierno del Estado, Tuxtla Gutiérrez, Chiapas, México.
——— and E. Hernández X. 1963. Los tipos de vegetación de México y su clasificación. Bol. Soc. Bot. Méx. 28: 29–179.

——— and A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31: 313–333.

Mittermeier, R. A., N. Myers, P. R. Gil, and C. G. Mittermeier. 2000. Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. Cemex, Conservation International and Agrupación Sierra Madre, Monterrey, Mexico.

Monasterio, M. (ed.). 1980. Estudios Ecológicos en los Páramos Andinos. Ediciones Universidad de Los Andes, Mérida, Venezuela.

Mora, M., R. Bernal, T. Croat, and J. Jácome. 2006. A phytogeographic analysis of Araceae of Cabo Corrientes (Chocó, Colombia) and comparable lowland tropical American floras. Ann. Missouri Bot. Gard. 93: 359–366.

Morellato, L. P. C. and C. F. B. Haddad (eds.). 2000. The Brazilian Atlantic forest. Biotropica (Special Issue) 32: 786–956.

Morello, J. 1958. La provincia fitogeográfica del monte. Opera Lilloana 2: 1–155.

Mori, S. A., B. M. Boom, and G. T. Prance. 1981. Distribution patterns and conservation of eastern Brazilian coastal forest tree species. Brittonia 33: 233–245.

———, ———, A. M. de Carvalho, and T. S. dos Santos. 1983. Southern Bahian moist forests. Bot. Rev. 49: 155–232.

——— et al. (+ 5 authors). 1997 et seq. Guide to the Vascular Plants of Central French Guiana. Part 1. Pteridophytes, Gymnosperms, and Monocotyledons. 2002. Part 2. Dicotyledons. New York Botanical Garden Press, Bronx.

Morley, R. J. 2000. Origin and Evolution of Tropical Rain Forests. Wiley & Sons, New York.

Morrone, J. J. 2000. Biogeographic delimitation of the subantarctica subregion and its provinces. Revista Mus. Argent. Ci. Nat., n.s., 2: 1–15.

Moscoso, R. M. 1943. Catalogus Florae Dominguensis. Parte I, Spermatophyta. L. & S. Printing, New York. [Sometimes cited as Publicación 24, Universidad Santo Domingo, Santo Domingo, Dominican Republic.]

Mostacero León, J., F. Mejía Coico, and O. Gamarra Torres. 2002. Taxonomía de las fanerogamas útiles del Peru. CONCYTEC, Trujillo, Peru.

Muldavin, E. H. 2002. Some floristic characteristics of the northern Chihuahuan Desert: A search for its northern boundary. Taxon 51: 453–462.

Muller, J. 1959. Palynology of Recent Orinoco Delta and shelf sediments: Reports of the Orinoco Shelf Expedition; Vol. 5. Micropaleontology 5: 1–32.

Murphy, L. S. 1916. Forests of Porto Rico, past, present, and future and their physical and economic development. U.S.D.A. Bull. 354: 1–99.

Myers, C. W. 1969. The ecological geography of cloud forest in Panama. Amer. Mus. Novit. 2396: 1–52.

Myers, N. 1991. Four for the forest's future. BioScience 41: 511–512. [Review of Gentry (1990), Four Neotropical Rainforests.]

———. 2003. Biodiversity hotspots revisited. BioScience 53: 916–917.

———, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nadkarni, N. M. and N. T. Wheelwright (eds.). 2000. Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, Oxford, U.K.

Navarro, G. and M. Maldonado. 2002. Geografía Ecológica de Bolivia: Vegetación y Ambientes Acuáticos. Fundación Simón I. Patiño, Cochabamba, Bolivia.

Nee, M. 2004. Flora de la Región del Parque Nacional Amboró. Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Nixon, K. C. and W. L. Crepet. 1989. *Trigonobalanus* (Fagaceae): Taxonomic status and phylogenetic relationships. Amer. J. Bot. 76: 828–841.

Nogueira Rodal, M. J. 2002. Montane forests in northeast Brazil: A phytogeographical approach. Bot. Jahrb. Syst. 124: 3–12.

Nores, M. and M. M. Cerana. 1990. Biogeography of forest relics in the mountains of northwestern Argentina. Revista Chilena Hist. Nat. 63: 37–48.

Novaes Pinto, M. 1994. Cerrado: Caracterização, Ocupacão e Perspectivas. 2nd ed. Editora Universidade de Brasília, Brasília.

Odum, H T. (ed.). 1970. A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico. Division of Technical Information, U.S. Atomic Energy Commission, Washington, D.C. pp. B147–B150.

Oersted, A. S. 1871. L'Amérique centrale. Recherches sur sa flore et sa géographie physique: Résultats d'un voyage dans les etats de Costa Rica et de Nicaragua, exécuté pendant les années 1846–1848. Copenhagen.

O'Hanley, D. S. 1996. Serpentinites: Recorders of Tectonic and Petrological History. Oxford University Press, Oxford, U.K.

Oliveira, P. S. and R. J. Marquis (eds.). 2002. The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York.

Oliveira-Filho, A. T. and M. A. L. Fontes. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *In:* L. P. C. Morellato and C. F. B. Haddad (eds.), The Brazilian Atlantic Forest. Biotropica (Special Issue) 32: 793–810.

——— and J. A. Ratter. 1995. A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. Edinburgh J. Bot. 52: 141–194.

——— and ———. 2002. Vegetation physiognomies and woody flora of the cerrado biome. *In:* P. S. Oliveira and R. J. Marquis (eds.), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. pp. 91–120.

ONERN (Oficina Nacional de Evaluación Recursor Naturales). 1976. Mapa Ecológico del Peru, Lima. Escala 1:1,000,000.

Osborne, P. L. 2000. Tropical Ecosystems and Ecological Concepts. Cambridge University Press, Cambridge, U.K.

Padoch, C., J. Márcio Ayres, M. Pinedo-Vasquez, and A. Henderson (eds.). 1999. Várzea: Diversity, Development, and Conservation of Amazonia's Whitewater Floodplains. New York Botanical Garden Press, Bronx.

Palacios-Chávez, R., B. Ludlow-Wiechers, and R. Villanueva G. 1991. Flora Palinológica de La Reserva de la Biosfera de Sian Ka'an, Quintana Roo, México. Centro de Investigaciones de Quintana Roo, Chetumal, México.

Park, O., A. Barden, and E. Williams. 1940. Studies in nocturnal ecology 9. Further analysis of activity of Panama rain forest animals. Ecology 21: 122–134.

Parker, T. A., III. 1993. The Lowland Dry Forests of Santa Cruz, Bolivia: A Global Conservation Priority. Rapid Assessment Program, Working Paper 4. Conservation International, Washington, D.C.

Parrotta, J. A., J. K. Francis, and R. Rolo de Almeida. 1995. Trees of the Tapajos: A Photographic Field Guide. International Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Pastorino, M. J. and L. A. Gallo. 2002. Quaternary evolutionary history of *Austrocedrus chilensis*, a cypress native to the Andean-Patagonian forest. J. Biogeogr. 29: 1167–1178.

Pennington, R. T., D. A. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forests and Pleistocene vegetation changes. J. Biogeogr. 27: 261–273.

Pennington, T. D. and J. Sarukhán K . 1998. Árboles Tropicales de México. 2nd ed. Universidad Nacional Autónoma de México, Fondo de Cultura Económica, México, D.F.

———, C. Reynel, and A. Daza. 2004. Illustrated Guide to the Trees of Peru. David Hunt, Sherborne, U.K.

Pennisi, E. 2001. Turmoil behind the exhibits. Science 293: 194–198. [See Jewels in the Crown III: Tropical Research Center.]

Peters, C. M. 1999. Introduction [Section 2: Forests and Forestry]. *In:* C. Padoch, J. Márcio Ayres, M. Pinedo-Vasquez, and A. Henderson (eds.), Várzea: Diversity, Development, and Conservation of Amazonia's Whitewater Floodplains. New York Botanical Garden Press, Bronx. pp. 115–118.

Philips Guides. 2002. National Parks, Brazil. Horizonte Geographico, São Paulo.

Phillips, O. and J. S. Miller. 2002. Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set. Monogr. Syst. Bot. Missouri Bot. Gard. 89.

Phillips, S., G. E. Rouse, and R. M. Bustin. 1997. Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panamá. Palaeogeogr. Palaeoclimatol. Palaeoecol. 128: 301–338.

Pimm, S. L. 2001. The World According to Pimm: A Scientist Audits the Earth. McGraw-Hill, New York.

——— and P. H. Raven. 2000. Extinction by numbers. Nature 403: 843–845.

Piperno, D. R. 1988. Phytolith Analysis. Academic Press, London.

Pires, J. M. 1973. Tipos de vegetacão da Amazonia. Publ. Avulsas Mus. Paraense Emilio Goeldi 20: 179–202.

——— and G. T. Prance. 1985. The vegetation types of the Brazilian Amazon. *In:* G. T. Prance and T. E. Lovejoy (eds.), Key Environments, Amazonia. Pergamon Press, Oxford, U.K. pp. 109–145.

Pitman, N. C. A. and P. M. Jørgensen. 2002. Estimating the size of the world's threatened flora. Science 298: 989.

Pittier, H. 1908. Ensayo sobre Plantas Usuales de Costa Rica. 2nd ed., reprinted 1957. University of Costa Rica, San José.

Platt, R. S. 1938. Items in the regional geography of Panama: With some comments on contemporary geographic method. Ann. Assoc. Amer. Geogr. 28: 28.

Por, F. D. 1992. Sooretama: The Atlantic Rain Forest of Brazil. SPB Academic Publishing, Den Haag, The Netherlands.

———. 1995. The Pantanal of Mato Grosso (Brazil). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Porter, D. M. 1973. The vegetation of Panama: A review. *In:* A. Graham (ed.), Vegetation and Vegetational History of Latin America. Elsevier Science Publishers, Amsterdam. pp. 167–201.

Prado, D. E. 1993. What is the Gran Chaco vegetation in South America? I. A Review. Contribution to the study of flora and vegetation of the chaco. V. Candollea 48: 145–172.

———. 2000. Seasonally dry forests of tropical South America: From forgotten ecosystems to a new phytogeographic unit. Edinburgh J. Bot. 57: 437–461.

——— and P. E. Gibbs. 1993. Patterns of species distributions in the dry seasonal forests of South America. Ann. Missouri Bot. Gard. 80: 902–927.

———, ———, A. Pott, and V. J. Pott. 1992. The chaco–pantanal transition in southern Mato Grosso, Brazil. *In:* P. A. Furley, J. Proctor, and J. A. Ratter (eds.), Nature and Dynamics of Forest–Savanna Boundaries. Chapman & Hall, London. pp. 451–470.

Prance, G. T. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31: 26–38.

———. 1987. Biogeography of neotropical plants. *In:* T. C. Whitmore and G. T. Prance (eds.), Biogeography and Quaternary History in Tropical America. Clarendon Press, Oxford, U.K. pp. 46–65.

———. 1989. American tropical forests. *In:* H. Leith and M. J. A. Werger (eds.), Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies. Ecosystems of the World 14B. Elsevier Science Publishers, Amsterdam. pp. 99–132.

———. 1990. The floristic composition of the forests of central Amazonian Brazil. *In:* A. H. Gentry (ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT. pp. 112–140.

———. 1996. Islands in Amazonia. Philos. Trans., Ser. B 351: 823–833.

——— and S. Brown Jr. 1987. Soils and vegetation. *In:* T. C.

Whitmore and G. T. Prance (eds.), Biogeography and Quaternary History in Tropical America. Clarendon Press, Oxford, U.K. pp. 19–45.

——— and G. B. Schaller. 1982. Preliminary study of some vegetation types of the pantanal, Mato Grosso, Brazil. Brittonia 34: 228–251.

Premoli, A. C., T. Kitzberger, and T. T. Veblen. 2000. Isozyme variation and recent biogeographical history of the long-lived conifer *Fitzroya cupressoides*. J. Biogeogr. 27: 251–260.

Proctor, G. R. 1985. Ferns of Jamaica: A Guide to the Pteridophytes. British Museum (Natural History), Publ. No. 895. London.

———. 1989. Ferns of Puerto Rico and the Virgin Islands. Mem. New York Bot. Gard. 53: 1–389.

Projecto RADAM. 1973–1975. Levantamento de Recursos Naturais. Vols. 1–7. Ministério de Minas e Energía, Rio de Janeiro.

Projeto RADAMBrasil. 1975–1985. Levantamento de Recursos Naturais. Vol. 8. Ministério de Minas e Energía, Rio de Janeiro.

PRORADAM (Proyecto Radargrametrico del Amazonas). 1979. La Amazonia Colombiana y Sus Recursos. 4 Vols. República de Colombia, Bogotá.

Puig, H. and R. Bracho. 1987. El Bosque Mesófilo de Montaña de Tamaulipas. Instituto de Ecología, México, D.F.

Ramella, L. and R. Spichiger. 1989. Interpretación preliminar del medio físico y de la vegetación del chaco boreal. Contribución al estudio de la flora y de la vegetación del chaco. I. Candollea 44: 639–680.

Rangel-Ch., J. O. (ed.) 2000. Colombia, Diversidad Biótica III, La Región de Vida Paramuna. Universidad Nacional de Colombia, Bogotá.

———, P. D. Lowy C., and M. Aguilar P. 1997. Colombia, Diversidad Biótica II, Tipos de Vegetación en Colombia. Editorial Guadalupe, Bogotá.

Ratter, J. A., A. Pott, V. J. Pott, C. N. Cunha, and M. Haridasan. 1988. Observations on woody vegetation types in the pantanal and at Corumbá, Brazil. Notes Roy. Bot. Gard. Edinburgh 45: 503–525.

———, P. W. Richards, G. Argent, and D. R. Gifford. 1973. Observations on the vegetation of northeast Mato Grosso: I. The woody vegetation types of the Xavantina–Cachimbo Expedition area. Philos. Trans., Ser. B 266: 449–492.

Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. 38: 151–177.

———. 1971. The relationships between 'Mediterranean' floras. *In:* P. H. Davis, P. C. Harper, and I. C. Hedge (eds.), Plant Life of South-west Asia. Royal Botanic Garden, Edinburgh. pp. 119–134.

——— (ed.). 1997. Nature and Human Society: The Quest for a Sustainable World. National Academy Press, Washington, D.C.

Reimold, R. J. and W. H. Queen (eds.). 1974. Ecology of Halophytes. Academic Press, London.

Renner, S. S., H. Balslev, and L. B. Holm-Nielsen. 1990. Flowering plants of Amazonian Ecuador—A checklist. AAU Reports 24. Botanical Institute, University of Aarhus, Aarhus, Denmark.

Ribeiro, J. F. and B. M. T. Walter. 1998. Fitofisionomias do bioma cerrado. *In:* S. M. Sano and S. P. Almeida (eds.), Cerrado: Ambiente e Flora. 2nd ed. Embrapa-CPAC, Planaltina, Brazil.

Richards, P. W. 1936. Ecological observations on the rain forest of Mount Dulit, Sarawak, I, II. J. Ecol. 24: 1–37, 340–360.

———. 1952. The Tropical Rain Forest: An Ecological Study. Cambridge University Press, Cambridge, U.K.

——— (with contributions by R. P. D. Walsh, I. C. Baillie, and P. Greig-Smith). 1996. The Tropical Rain Forest. 2nd ed. Cambridge University Press, Cambridge, U.K.

———, A. G. Tansley, and A. S. Watt. 1940. The recording of structure, life form and flora of tropical forest communities as a basis for their classification. J. Ecol. 28: 224–239. (also published as Imp. For. Inst. Paper No. 19, Oxford, U.K., 1939).

Richardson, D. M. (ed.). 1998. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, U.K. (Paperback edition, 2000).

Romero, E. J. 1977. Polen de gimnospermas y fagáceas de la Formación Río Turbio (Eoceno), Santa Cruz, Argentina. Fundación para la Educación, La Ciencia y La Cultura, Buenos Aires.

Rose, W. I. 2001. Volcanic irony, hard lessons from the dark side of volcanology (review of Bruce, 2001 and Williams and Montaigne, 2001). Nature 411: 21–22.

Roth, L. C. and A. Grijalva. 1991. New record of the mangrove *Pelliciera rhizophorae* (Theaceae) on the Caribbean coast of Nicaragua. Rhodora 93: 183–186.

Roubik, D. W. and J. E. Moreno P. 1991. Pollen and Spores of Barro Colorado Island. Monogr. Syst. Bot. Missouri Bot. Gard. 36 (http://striweb.si.edu/roubik).

Rudas Lleras, A. and A. Prieto Cruz. 2005. Flórula del Parque Nacional Natural Amacayacu, Amazonas, Colombia. Monogr. Syst. Bot. Missouri Bot. Gard. 99.

Rushing, A. E. 1985. Spore morphology in the genus *Bruchia* Schwaegr. (Musci). Amer. J. Bot. 72: 75–85.

Rzedowski, J. 1973. Geographical relationships of the flora of Mexican dry regions. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 61–72.

———. 1978. Vegetación de México. Editorial Limusa, México, D.F.

———. 1991. Diversidad y orígenes de la flora fanerogámica de México. Acta Bot. Mex. 14: 3–21.

——— and R. McVaugh. 1966. La Vegetación de Nueva Galicia. Contrib. Univ. Michigan Herb. 9: 1–123.

——— and G. C. de Rzedowski. 1979. Flora Fanerogámica del Valle de México, Vol. 1. Escuela Nacional de Ciencias Biológicas, Instituto de Ecología, México, D.F.

——— and ———. 1985. Flora Fanerogámica del Valle de

México, Vol. 2. Escuela Nacional de Ciencias Biológicas, Instituto de Ecología, México, D.F.

——— and ———. 1990. Flora Fanerogámica del Valle de México, Vol. 3. Escuela Nacional de Ciencias Biológicas, Instituto de Ecología, México, D.F.

Sagástegui Alva, A., I. Sánchez Vega, M. Zapata Cruz, and M. O. Dillon. 1999 et seq. Diversidad Floristica del Norte de Perú. Graficart, Trujillo, Perú.

Sanford, R. L., Jr., P. Paaby, J. C. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. *In:* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago. pp. 19–33.

Santiago-Valentin, E. and R. G. Olmstead. 2004. Historical biogeography of Caribbean plants: Introduction to current knowledge and possibilities from a phylogenetic perspective. Taxon 53: 299–319.

Sarmiento, F. O. 2001. Ecuador. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 497–548.

Sarmiento, G. 1983. The savannas of tropical America. *In:* F. Bourlière (ed.), Tropical Savannas. Ecosystems of the World 13. Elsevier Science Publishers, Amsterdam. pp. 245–288.

——— (translated by O. Solbrig). 1984. The Ecology of Neotropical Savannas. Harvard University Press, Cambridge, MA.

Sawyer, J. O. and A. A. Lindsey. 1971. Vegetation of the life zones in Costa Rica. Monograph 2, Indiana Academy of Science, Indianapolis.

Scarano, F. R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Ann. Bot. 90: 517–524.

Schery, R. W. 1942. A few facts concerning the flora of Panama. Chron. Bot. 7: 77–79.

Schimper, A. F. W. 1903. Plant Geography upon a Physiological Basis. Oxford University Press, Oxford, U.K.

Schjellerup, I. 1992. Pre-Columbian field systems and vegetation in the jalca of northeastern Peru. *In:* H. Balslev and J. L. Luteyn (eds.), Páramo: An Andean Ecosystem Under Human Influence. Academic Press, London, U.K. pp. 137–150.

Schnee, L. 1973. Plantas Comunes de Venezuela. Universidad Central de Venezuela, Facultad de Agronomía, Maracay.

Schubert, C. and O. Huber. 1989. The Gran Sabana: Panorama of a Region. Lagoven Booklets (Filiae de Petróleos de Venezuela, SA), Caracas. [Spanish and English versions.]

Schulman, E. 1956. Dendroclimatic Changes in Semiarid America. University of Arizona Press, Tucson.

Seeliger, U. (ed.). 1992. Coastal Plant Communities of Latin America. Academic Press, London.

Seemann, B. 1854. The Botany of the Voyage of *H.M.S. Herald*. Reeve and Co., London [Includes Flora of the Isthmus of Panama.]

Shreve, F. and I. L. Wiggins. 1964. Vegetation and Flora of the Sonoran Desert. 2 vols. Stanford University Press, Stanford, CA.

Shuttleworth, W. J. et al. (+ 14 authors). 1984. Eddy correlation measurements of energy partition for Amazonian forest. Quart. J. Royal Meterol. Soc. 110: 1143–1162.

Sierra, R. 1999a. Vegetación remanente del Ecuador continental circa 1996. Escala 1:1,000,000. Proyecto INEFAN/GEF y Wildlife Conservation Society. EcoCiencia, Quito.

——— (ed.). 1999b. Propuesta Preliminar de un Sistema de Classificación de vegetación para el Ecuador Continental. Proyecto INEFAN/GEF–BIRF y EcoCiencia, Quito.

———, C. Cerón, W. Palacios, and R. Valencia. 1999. Mapa de vegetación del Ecuador continental. Proyecto INEFAN/GEF-BIRF, Wildlife Conservation Society y EcoCiencia, Quito. Escala 1:1,000,000.

Sigurdsson, H. 2001. Not "a piece of cake." (Review of V. Bruce, 2001 and S. Williams and F. Montaigne, 2001.) Science 292: 643–644.

Silver, W. L., E. Marín-Spiotta, and A. E. Lugo. 2001. El Caribe. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 155–181.

Simpson, B. B. 1979. A revision of the genus *Polylepis* (Rosaceae: Sanguisorbeae). Smithsonian Contr. Bot. 43: 1–62.

Sioli, H. (ed.). 1984. The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Sipman, H. J. M. 1992. The origin of the lichen flora of the Colombian páramos. *In:* H. Balslev and J. L. Luteyn (eds.), Páramo: An Andean Ecosystem Under Human Influence. Academic Press, London. pp. 95–109.

Skvarla, J. J., J. R. Rowley, V. C. Hollowell, and W. F. Chissoe. 2003. Annulus-pore relationship in Gramineae (Poaceae) pollen: The pore margin of *Pariana*. Amer. J. Bot. 90: 924–930.

Solbrig, O. T. 1972. The floristic disjunctions between the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the United States. Ann. Missouri Bot. Gard. 59: 218–223.

Söyrinki, N. 1991. On the alien flora of the province of Buenos Aires, Argentina. Ann. Bot. Fenn. 28: 59–79.

Spichiger, R. (ed.). 1983 et seq. Flora del Paraguay. Conservatoire et Jardin Botaniques de la Ville de Genève, Geneva; Missouri Botanical Garden, St. Louis.

Standley, P. C. 1927. The flora of Barro Colorado Island. Smithsonian Misc. Collect. 78: 1–132.

———. 1928. Flora of the Panama Canal Zone. Contrib. U.S. Natl. Herb. 27: 1–416.

———. 1937–1938. Flora of Costa Rica. Field Museum of Natural History, Chicago.

——— and J. A. Steyermark. 1945. The vegetation of Guatemala, a brief review. *In:* F. Verdoorn (ed.), Plants and Plant Sciences in Latin America. Ronald Press, New York. pp. 275–278.

Stannard, B. L. (ed.). 1995. Flora of the Pico das Almas, Chapada Diamantina, Bahia, Brazil. Royal Botanic Gardens, Kew, Richmond, U.K.

Steele, A. R. 1964. Flowers for the King: The Expedition of Ruiz and Pavón and the Flora of Peru. Duke University Press, Durham, NC.

Stehlé, H. 1945. Forest types of the Caribbean islands. Part 1. Caribbean Forester 6 (Suppl.): 273–422.

———. 1946. Les types forestiers des îles Caraibes. Caribbean Forester 7 (Suppl.): 337–709.

Stevens, W. D. 2001. Fitogeografía. *In:* W. D. Stevens, C. Ulloa Ulloa, A. Pool, and O. M. Montiel (eds.), Flora de Nicaragua. Missouri Botanical Garden Press, St. Louis. pp. xxxiii–xxxv.

———, C. Ulloa Ulloa, A. Pool, and O. Montiel (eds.). 2001. Flora de Nicaragua. Missouri Botanical Garden Press, St. Louis.

Steyermark, J. 1950. Flora of Guatemala. Ecology 31: 368–372.

———, P. E. Berry, and B. K. Holst (gen. eds.). 1995 et seq. Flora of the Venezuelan Guayana. Missouri Botanical Garden Press, St. Louis; Timber Press, Portland.

——— and O. Huber. 1978. Flora del Ávila. Sociedad Venezolana Ciencias Naturales, Caracas.

Swarts, F. A. (ed.). 2000. The Pantanal: Understanding and Preserving the World's Largest Wetland. Paragon House, St. Paul, MN.

Talbot, L. M. and R. H. Kesel. 1975. The tropical savanna ecosystem. Geosci. & Man 10: 15–26.

Tasaico, H. 1967. Ecología (zonas de vida de la República Dominica). *In:* Reconocimiento y evaluación de los recursos naturales de la República Dominicana (con el mapa ecológico 1:25,000). Tomo 1. Organización de Los Estados Americanos, Washington, D.C.

Taylor, R. J., T. F. Patterson, and R. J. Harrod. 1994. Systematics of Mexican spruce—Revisited. Syst. Bot. 19: 47–59.

Terborgh, J. 1990. An overview of research at Cocha Cashu Biological Station. *In:* A. H. Gentry (ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT. pp. 48–59.

Teunissen, P. A. and J. T. Wildschut. 1970. Vegetation and Flora of the Savannas in the Brickheuvel Nature Reserve, Northern Suriname. North Holland Publishing Co., Amsterdam.

Thornthwaite, C. W. 1948. An approach towards a rational classification of climate. Geogr. Rev. 38: 55–94.

Thrower, N. J. W. and D. E. Bradbury. 1977. Chile–California Mediterranean Scrub Atlas, a Comparative Analysis. US/IBP Synthesis Series 2. Dowden, Hutchinson & Ross, Stroudsbury, PA.

Ting, W. S. 1966. Determination of *Pinus* species by pollen statistics. Univ. Calif. Publ. Geol. Sci. 58: 1–182.

Toledo, V. M. 1985. A critical evaluation of the floristic knowledge in Latin America and the Caribbean. A Report presented to the Nature Conservancy: International Program. Washington, D.C.

Tomlinson, P. B. 1986. The Botany of Mangroves. Cambridge University Press, Cambridge, U.K.

Tosi, J. A., Jr. 1960. Zonas de Vida Natural en el Perú, Memoria Explicativa sobre el Mapa Ecológico del Perú. Proyecto 39, IICA-OEA. Bol. Tecn. No. 5. Lima.

———. 1964. Climatic control of terrestrial ecosystems: A report on the Holdridge model. Econ. Geogr. 40: 173–181.

———. 1983. Provisional Ecological Map of the Republic of Brazil. Tropical Science Center, San José, Costa Rica. Scale 1:10,000,000.

Trejo-Torres, J. C. and J. D. Ackerman. 2002. Composition patterns of Caribbean limestone forests: Are parsimony, classification, and ordination analyses congruent? Biotropica 34: 502–515.

Troll, C. 1968. Geo-Ecology of the Mountainous Regions of the Tropical Americas. UNESCO (*In*: Kommission bei Ferd. Dümmlers Verlag, Bonn.)

Tryon, A. F. and B. Lugardon. 1991. Spores of the Pteridophyta: Surface, Wall Structure, and Diversity Based on Electron Microscope Studies. Springer Verlag, Berlin.

Tryon, R. M. and R. G. Stolze. 1989 et seq. Pteridophyta of Peru. Fieldiana, Bot., n.s. 20.

——— and A. F. Tryon. 1982. Ferns and Allied Plants with Special Reference to Tropical America. Springer Verlag, Berlin.

Tuomisto, H. et al. (+ 6 authors). 2002. Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuní National Park, Ecuadorian Amazonia. Biotropica 34: 516–533.

Ulloa Ulloa, C., S. Álvarez Molina, P. M. Jørgensen, and D. Minga. 2004. Cien Plantas Silvestres del Páramo/One Hundred Wild Plants from the Páramo, Parque Nacional Cajas, Cuenca, Ecuador. Spanish/English edition. Etapa, Cuenca, Ecuador; Missouri Botanical Garden Press, St. Louis.

——— and P. M. Jørgensen. 1993. Árboles y Arbustos de los Andes del Ecuador. AAU Reports 30. Botanical Institute, University of Aarhus, Aarhus, Denmark.

Ungricht, S. 2004. How many plant species are there? And how many are threatened with extinction? Endemic species in global biodiversity and conservation assessments. Taxon 53: 481–484.

UNESCO. 1980–1981. Carte de la Végétation d'Amérique du Sud. Carte et Notice Explicative. UNESCO, Paris. Scale 1:5,000,000.

UNESCO-FAO. 1975. Carte Mondiale des Sols au 1/5,000,000. Vol. I. Légende, Paris.

UNOPS. 2001. Haiti Land Cover Map, categorization of 1990 SPOT satellite imagery of Haiti. Provided by ERIM under contract to United Nations Development Programme/ United Nations Office for Project Services, Project HAI/92/001, New York.

Urban, I. 1898–1928. Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis. Reprint, 1964, A. Asher, Amsterdam.

———. 1902. Vitae itineraque collectorum botanicorum. *In:* K. P. F. von Martius, Flora Brasiliensis 1: 1–152.

van der Hammen, T. 1983. *Trigobalanus* and the tropical amphi-Pacific element in the north Andean forest. J. Biogeogr. 10: 437–440.

——— and A. M. Cleef. 1986. Development of the high Andean páramo flora and vegetation. *In:* F. Vuilleumier and M. Monasterio (eds.), High Altitude Tropical Biogeography. Oxford University Press, Oxford, U.K. pp. 153–201.

van der Werff, H. and T. Consiglio. 2004. Distribution and conservation significance of endemic species of flowering plants in Peru. Biodivers. & Conservation 13: 1699–1713.

van Donselaar, J. 1969. Observations on savanna vegetation types in the Guianas. Vegetatio 17: 271–312.

Vásquez Martínez, R. (edited by A. R. Lleris and C. M. Taylor). 1997. Flórula de las Reservas Biológicas de Iquitos, Perú. Monogr. Syst. Bot. Missouri Bot. Gard. 63.

Vaughn, H. H., E. S. Deevey Jr., and S. E. Garrett-Jones. 1985. Pollen stratigraphy of two cores from the Petén Lake District, with an appendix on two deep-water cores. *In:* M. Pohl (ed.), Prehistoric Lowland Maya Environment and Subsistence Economy. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA. pp. 73–89.

Velázquez, A., V. M. Toledo, and I. Luna. 2000. Mexican temperate vegetation. *In:* M. G. Barbour and W. D. Billings (eds.), North American Terrestrial Vegetation. 2nd ed. Cambridge University Press, Cambridge, U.K. pp. 573–592.

Veloso, E. 1966. Tipos de vegetação. *In:* Atlas Forestal do Brasil. Ministério de Agricultura Conselho Forestal Federal, Rio de Janeiro.

Veloso, H. P. 1947. Considerações gerais sobre a vegetação do estado de Mato Grosso. II. Notas preliminares sobre pantanal e zonas de transição. Mem. Inst. Oswaldo Cruz 45: 253–272.

———, A. L. R. Rangel Filho, and J. C. A. Lima. 1991. Classificação da Vegetação Brasileira, Adaptada a Um Sistema Universal. Instituto Brasileiro de Geografía e Estatística, Rio de Janeiro.

Viksne, A., T. Liston, and C. D. Sapp. 1970. SLR reconnaissance of Panama. Photogramm. Eng. 36: 253–259.

Voronov, A. G. 1970. Mapa de vegetación. Atlas Nacional de Cuba. Havana.

Vuilleumier, F. and M. Monasterio (eds.). 1986. High Altitude Tropical Biogeography. Oxford University Press, Oxford, U.K.

Wadsworth, F. H. 1970. Review of past research in the Luquillo Mountains of Puerto Rico. *In:* H. T. Odum (ed.), A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico. Division of Technical Information, U.S. Atomic Energy Commission, Washington, D.C. pp. B33–B46.

Wagner, P. L. 1964. Natural vegetation of Middle America. *In:* R. C. West (ed.), Handbook of Middle American Indians. 1. Natural Environment and Early Cultures. University of Texas Press, Austin. pp. 216–264.

Walker, B. H. (ed.). 1987. Determinants of Tropical Savannas. IRL Press, Oxford, U.K.

Wallace, R. 2005. Going Ape Over an Amazon Treasure. Interview with Christiane Amanpour, *60 Minutes II*, CBS, February 2, 2005.

Walsh, R. P. D. 1996. Climate. *In:* P. W. Richards, The Tropical Rain Forest. 2nd ed. Cambridge University Press, Cambridge, U.K. pp. 159–205.

Warming, E. 1892. Lagoa Santa: Et bidrag til den biologiske plantegeographi. Kongel. Danske Vidensk. Selsk. 6.

———. 1909. Oecology of Plants. Clarendon Press, Oxford, U.K. [Translation P. Groom and I. B. Balfour, Arno Press, New York. 1977.]

Weber, H. 1958. Die Páramos von Costa Rica und ihre pflanzengeographische Verkettung mit den Hochandean Südamerikas. Akad. Wiss. Mainz, Abh. Math.-Naturwiss. Kl. 3: 1–78. [Weber, H. Los páramos de Costa Rica y su concatenación fitogeográficacion los Andes Suramericanos. Instituto Geográfico, San José, Costa Rica.]

———. 1969. Zur natürlichen Vegetations-gliederung von Südamerika. *In:* E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli (eds.), Biogeography and Ecology in South America. Dr. W. Junk Publishers, The Hague. pp. 475–518.

Webster, G. L. 1995. The panorama of neotropical cloud forests. *In:* S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn (eds.), Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden Press, Bronx. pp. 53–77.

Wendt, T. 1993. Composition, floristic affinities, and origins of the canopy tree flora of the Mexican Atlantic slope rain forests. *In:* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa (eds.), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, Oxford, U.K. pp. 595–680.

Whitesell, S., R. J. Lilieholm, and T. L. Sharik. 2002. A global survey of tropical biological field stations. BioScience 52: 55–64.

Wiggins, I. L. 1980. Flora of Baja California. Stanford University Press, Stanford, CA.

Wilbur, R. L. (and collaborators). 1994. Vascular plants: An interim checklist. Appendix 3. *In:* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago. pp. 350–378.

Wiley, S. C., A. V. Dodd, and J. V. Chambers. 1955. Environmental Handbook of Fort Sherman and Fort Gulick, Panama Canal Zone. U.S. Army Headquarters, Quartermaster Research Development Commission, Environmental Protection Division, Tech. Rept. EP-17, Natick, MA.

Wille, M., H. Hooghiemstra, R. Hofstede, J. Fehse, and J. Sevink. 2002. Upper forest line reconstruction in a deforested area in northern Ecuador based on pollen and vegetation analysis. J. Trop. Ecol. 18: 409–440.

Williams, S. and F. Montaigne. 2001. Surviving Galeras. Houghton Mifflin, Boston.

Wilson, E. O. and D. Perlman. 2000. Conserving Earth's biodiversity with E. O. Wilson. CD-ROM. Island Press, Washington, D.C.

Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. U.S. Geol. Survey Prof. Paper 1106: 1–37.

Woods, C. A. and F. E. Sergile (eds.). 2001. Biogeography of the West Indies: Patterns and Perspectives. CRC Press, Boca Raton, FL.

Woodson, R. E., Jr. (ed.). 1943–1981. Flora of Panama. Ann. Missouri Bot. Gard. 30 et seq.

Worbes, M. 1997. The forest ecosystem of the floodplains. *In:* W. Junk (ed.), The Central Amazon Floodplain: Ecology of a Pulsing System. Springer Verlag, Berlin. pp. 223–265.

Zamora, N., B. E. Hammel, and M. H. Grayum. 2004a. Vegetación/Vegetation. *In:* B. E. Hammel, M. H. Grayum, C. Herrera, and N. Samora (eds.), Manual de Plantas de Costa Rica, Vol. 1. Missouri Botanical Garden Press, St. Louis. pp. 91–216.

———, Q. Jiménez M., and L. J. Poved A. 2004b. Árboles de Costa Rica/Trees of Costa Rica. Vol. 3. INBio, Santo Domingo de Heredia, Costa Rica.

Zanoni, T. A. and W. R. Buck (eds.). 2005. Flora of the Greater Antilles Newsletter No. 20. New York Botanical Garden, Bronx.

———, C. R. Long, and G. McKiernan. 1984. Bibliografía de la flora y de la vegetación de la Isla Española. Moscosoa 3: 1–61.

Zuloaga, F. O. and O. Morrone (eds.). 1996. Catálogo de las Plantas Vasculares de la República Argentina. I. Pteridophyta, Gymnospermae y Angiospermae (Monocotyledoneae). II–1. (1999) Acanthaceae-Euphorbiaceae (Dicotyledonae). II–2. (1999) Fabaceae-Zygophyllaceae (Dicotyledonae). Monogr. Syst. Bot. Missouri Bot. Gard. 60, 74.

——— et al. (+5 authors). 1994. Catálogo de la Familia Poaceae en la República Argentina. Monogr. Syst. Bot. Missouri Bot. Gard. 47.

ADDITIONAL REFERENCES/GENERAL READINGS/ ELECTRONIC ADDRESSES

Abbott, A. 2004. A world of learning. Nature 431: 631. [Announces re-publication of Alexander von Humboldt's works by Eichborn Publishing, Frankfurt.]

Acevedo-Rodríguez, P. (and collaborators). 1996. Flora of St. John, U.S. Virgin Islands. New York Botanical Garden Press, Bronx.

——— and M. T. Strong. 2005. Monocotyledons and Gymnosperms of Puerto Rico and the Virgin Islands. Contrib. U.S. Natl. Herb. 52: 1–415.

Allen, W. H. 1996. Traveling across the treetops, a crane's-eye view of Panama's forest canopy yields biological surprises. BioScience 46: 796–799.

Alves, R., V. Filho, and M. D. Machado. 2007. Is classical taxonomy obsolete? Taxon 56: 287–288.

Anderson, E. F. 1996. Peyote: The Divine Cactus. University of Arizona Press, Tucson.

Andes Biodiversity Resources and Information. http://www.andesbiodiversity.org.

Anonymous. 1990. Botanical Research and Management in Galápagos. Missouri Botanical Garden Press, St. Louis.

———. 2002. Flooded kingdom (matters of size: the pantanal). Nat. Conservancy Spring: 22–23.

———. 2002. Genomics and taxonomy for all. Nature 417: 573.

Araújo, M. B. and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313: 1396–1397.

Arbingast, S. A. (+ 8 authors). 1975. Atlas of Mexico. Bureau of Business Research, University of Texas, Austin.

Arizona-Sonora Desert Museum. 1999. A Natural History of the Sonoran Desert. University of California Press, Berkeley, published in collaboration with the Arizona-Sonora Desert Museum Press, Tucson.

Asner, G. P. et al. (+ 5 authors). 2002. Estimating canopy structure in an Amazon forest from laser range finder and IKONOS satellite observations. Biotropica 34: 483–492.

Asociación Latinoamericana de Botánica. Web site of the ALB. http://www.botanica-ALB.org.

Azuma, H., J. G. García-Franco, V. Rico-Gray, and L. B. Thien. 2001. Molecular phylogeny of the Magnoliaceae: The biogeography of tropical and temperate disjunctions. Amer. J. Bot. 88: 2275–2285.

Baker, W. J. and S. Zona (eds.). 2006. Proceedings of The Palms—An International Symposium on the Biology of the Palm Family. Bot. J. Linn. Soc. 151: 2–163.

Banke, V. 1991. The Pantanal: Brazil's Forgotten Wilderness. Sierra Club Books, San Francisco.

Basualdo, I. and N. Soria (eds.). 2004. 100 Especies del Cerrado en Paraguay. Facultad de Ciencias Químicas-UNA, San Lorenzo, Paraguay; Missouri Botanical Garden Press, St. Louis.

Batalha, M. A. and F. R. Martins. 2002. The vascular flora of the cerrado in Emas National Park (Goiás, central Brazil). Sida 20: 295–311.

Bawa, K. S. et al. (+ 8 authors). 2004. Letters: Tropical ecosystems into the 21st century. Science 306: 227–228.

Beattie, A. and P. R. Ehrlich. 2001. Wild Solutions: How Biodiversity is Money in the Bank. Yale University Press, New Haven, CT.

Beletsky, L. (ed.). 1998 et seq. The Ecotravellers' Wildlife Guides. Academic Press, London. [Belize, Costa Rica, Ecuador, Mexico.]

Belt, T. 1985. The Naturalist in Nicaragua. University of Chicago Press, Chicago. [Foreword by D. H. Janzen; originally published 1888, Edward Bumpas, London.]

BioNet International. http://www.bionet-intl.org/opencms/opencms/caseStudies/default.jsp. [Case studies on the value of taxonomy.]

Bisby, F. A., J. Shimura, M. Ruggiero, J. Edwards, and C. Haeuser. 2002. Taxonomy, at the click of a mouse. Nature 418: 367. [Informatics and taxonomy are working together to achieve more than either could alone.]

Blackmore, S. 2002. Biodiversity update—Progress in taxonomy. Science 298: 365.

Bletter, N., J. Janovec, B. Brosi, and D. C. Daly. 2004. A digital base map for studying the neotropical flora. Taxon 53: 469–477. ["GIS and the American Base Map can aid and accelerate techniques used in historical biogeography (e.g., Crisci et al., 2003). ArcView streamlines the chore of scoring the occurrence of species in a set of defined geographic areas because it is relatively easy to circumscribe sets of areas (by drawing polygons on the base map for each area) and generate the necessary matrix of taxa occurrence vs. area using the Link function. The base map enhances the researcher's versatility in testing biogeographic hypotheses, because it is also possible to derive sets of areas from existing layers of the map (e.g., Ecoregions, topography, precipitation regimes," p. 475).]

Bonifaz, C. and X. Cornejo. 2004. Flora del Bosque de Garúa (árboles y epifitas) de la comuna Loma Alta, Cordillera Chongón Colonche, Provincial de Guayas, Ecuador. Universidad de Guayaquil, Guayaquil.

Bosques Tropicales Estacionalmente Secos. http://www.geocities.com/bosquesecos/bibliografia.htm. [List of literature on dry Neotropical forests.]

Botanicus Digital Library. Missouri Botanical Garden. http://www.botanicus.org/. [A Web-based encyclopedia of historic botanical literature.]

Botanische Staatssammlung München. Natural History Collection. http://www.botanischestaatssammlung.de. [Images of Asteraceae nomenclatural types are included under "Projects" and "Infocomp."]

Botany of the Maya Area. 1936–1940. Carnegie Institution of Washington Misc. Papers.

Breedlove, D. E. and R. M. Laughlin. 2000. The Flowering of Man: A Tzotzil Botany of Zinacantán. Smithsonian Institution Press, Washington, D.C.

Bridges, E. L. 1987. Uttermost Part of the Earth. Century, London. [Patagonia.]

Bridgewater, S., R. T. Pennington, C. A. Reynel, A. Daza, and T. D. Pennington. 2003. A preliminary floristic and phytogeographic analysis of the woody flora of seasonally dry forests in northern Peru. Candollea 58: 129–148.

British Library. 2001. Rain Forest Requiem, Recordings of Wildlife in the Amazon Rainforest by Richard Ranft. CD, British Library National Sound Archive, London, U.K. [Wildlife Section, National Sound Archive, The British Library, 96 Euston Road, London NW1 2DB, U.K.; nsa-wildsound@bl.uk. See also, Sir David Attenborough, 1999, Endangered Nature, The Century in Sound, ibid.]

Brook, B. W., N. S. Sodhi, and P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424: 420–426. [Inferred losses 80%.]

Brooks, T. M. et al. (+ 8 authors). 2006. Global biodiversity conservation priorities. Science 313: 58–61.

Bubb, P. 2001. Desarrollo de una base de datos para los bosques nublados del neotrópico. *In:* M. Kappelle and A. D. Brown (eds.), Bosques Nublados del Neotrópico. INBio, Santo Domingo de Heredia, Costa Rica. pp. 51–62.

Burger, W. 1980. Why are there so many kinds of flowering plants in Costa Rica? Brenesia 17: 371–388.

Butler, D. 2006. Murders halt rainforest research. Nature 441: 555.

Campbell, D. G. and H. D. Hammond (eds.). 1989. Floristic Inventory of Tropical Countries: The Status of Plant Systematics, Collections, and Vegetation, Plus Recommendations for the Future. New York Botanical Garden Press, Bronx.

Cantú, C., R. G. Wright, M. Scott, and E. Strand. 2004. Assessment of current and proposed nature reserves of Mexico based on their capacity to protect geophysical features and biodiversity. Biol. Conservation 115: 411–417.

Carmona, A. 2007. A conversation on conservation: Contemplating the impact of climate change in the Latin-America-Caribbean region. http://www.coha.org/2007/08/a-conversation-on-conservation-contemplating-the-impact-of-climate-change-in-the-Latin-America-Caribbean-region.

Challenger, A. (con la colaboración de J. Caballero). 1998. Utilización y Conservación de los Ecosistemas Terrestres de México: Pasado, Presente y Futuro. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F.

Chambers, J. Q., N. Higuchi, and J. P. Schimel. 1998. Ancient trees in Amazonia. Nature 391: 135–136. [Maximum age fide ^{14}C, ~1400 years.]

Chapin, F. S. (ed.). 2001. Global Biodiversity in a Changing Environment: Scenarios for the 21st Century. Springer Verlag, Berlin.

Chazdon, R. L. and T. Whitmore (eds.). 2002. Foundations of Tropical Forest Biology: Classic Papers with Commentaries. University of Chicago Press, Chicago.

Chihuahuan Desert Discovery, Magazine of the Chihuahuan Desert Research Institute. 1975 et seq. Fort Davis, TX.

Chiles, J. R. 1992. High-tech conservation, information-age tools have revolutionized the work of ecologists. Nat. Conservancy July/August, 42: 15–24.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.). 2001. Dispersal. Oxford University Press, Oxford, U.K.

Cohn, J. P. 2001. Sonoran Desert conservation. BioScience 51: 606–610.

Cole, S. 2007. Long-term increase in rainfall seen in tropics.

http://www.nasa.gov/centers/goddard/news/topstory/2007/rainfall_increase.html.
Colwell, R. K. 2004. Biota 2, The Biodiversity Database Manager. Sinauer Associates, Sunderland, MA.
Conservation Commons. http://www.conservationcommons.org. [Web site containing conservation-related information.]
Conservatory and Botanic Garden of Geneva. http://www.ville-ge.ch/musinfo/bd/cjb/auxilium/index.php. [Web site containing signatures, labels, and letters of famous botanists.]
Conserve Online. A Guide to Caribbean Vegetation Types. http://conserveonline.org/library/A_Guide_to_Caribbean_Vegetation_Types.doc/view.html.
Coyne, J. A. 2005. Review: Endless forms most beautiful: The New science of evo-devo, by S. B. Carroll. Nature 435: 1029–1030. [Switching on evolution, how does evo-devo explain the high diversity of life on Earth?]
Craw, R. C., J. R. Grehan, and M. J. Heads. 1999. Panbiogeography. Oxford University Press, Oxford, U.K.
Crawford, A. J., E. Bermingham, and C. Polanía S. 2007. The role of tropical dry forest as a long-term barrier to dispersal: A comparative phylogeographical analysis of dry forest tolerant and intolerant frogs. Molec. Ecol. 16: 4789–4807.
Dallmeier, F. and J. A. Comiskey (eds.). 1998. Forest Biodiversity in North, Central and South America, and the Caribbean. Man and the Biosphere series, Vol. 21. UNESCO Press, New York.
Dalton, R. 2001. Earth sciences and biodiversity fall victim to budget plan. Nature 410: 854.
———. 2005. Saving the agave. Nature 438: 1070–1071.
———. 2006. Cashing in on the rich coast. Nature 442: 567–569.
Dean, W. 1997. With Broadax and Firebrand: The Destruction of the Brazilian Atlantic Forest. University of California Press, Berkeley.
Dingle, H. 1996. Migration: The Biology of Life on the Move. Oxford University Press, Oxford, U.K.
Discover Life. http://www.discoverlife.org. [Web site with links to nature guides, global mapper, conservation, invasives, etc. Served from the University of Georgia, Missouri Botanical Garden, and Smithsonian Tropical Research Institute.]
Dodd, R. S. (ed.). 1999. Diversity and Function in Mangrove Ecosystems. Developments in Hydrobiology 145, Hydrobiologia vol. 413. Kluwer Academic Publishers, Dordrecht, The Netherlands.
Dodson, C. H. et al. 1989. Icones Plantarum Tropicarum, Series II. Missouri Botanical Garden Press, St. Louis. [Orchidaceae.]
Downie, A. 2001. Resurrection, Brazil's Atlantic forest rises from the ashes. Nat. Conservancy July/August: 23–29.
Dransfield, J. et al. (+ 5 authors). 2005. A new phylogenetic classification of the palm family, Arecaceae. Kew Bull. 60: 559–569.
Edwards, E. J., R. Nyffeler, and M. J. Donoghue. 2005. Basal cactus phylogeny: Implications of *Pereskia* (Cactaceae) paraphyly for the transition to the cactus life form. Amer. J. Bot. 92: 1177–1188.
Ehrlich, P. R. and E. O. Wilson. 1991. Biodiversity studies: Science and policy. Science 253: 758–762.
Emory, J. 1990. Brazil's pantanal, "that land of wonderful inundation." Nat. Conservancy September/October: 7–14.
Enright, N. J. and R. S. Hill (eds.). 1996. Ecology of the Southern Conifers. Smithsonian Institution Press, Washington, D.C.
Estrada C., A. E. Martínez, and A. Martínez M. 2003. Los Géneros de Leguminosas del Norte de México. BRIT Press, Fort Worth.
Evenari, M., I. Noy-Meir, and D. W. Goodall (eds.). 1985. Hot Deserts and Arid Shrublands, A. Ecosystems of the World 12A. Elsevier Science Publishers, Amsterdam.
Ewan, J. 1989. Five American naturalists on the Andes and Amazonia: A study in personality. Arch. Nat. Hist. 16: 1–14.
———. 1992. Through the jungle of Amazon travel narratives of naturalists. Arch. Nat. Hist. 19: 185–207.
Ewel, J. J. and J. L. Whitmore. 1973. The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands. Forest Service Research Paper ITF-18, Institute of Tropical Forestry, Río Piedras, Puerto Rico.
FAO. 2007. State of the World's Forest 2007. Food and Agriculture Organization of the United Nations, Rome.
Farjon, A. (ed.). 2005. A Monograph of Cupressaceae and *Sciadopitys*. Royal Botanic Gardens, Kew, Richmond, U.K.
———. 2005. A Bibliography of Conifers. 2nd ed. Royal Botanic Gardens, Kew, Richmond, U.K.
——— and B. T. Styles. 1997. *Pinus* (Pinaceae). New York Botanical Garden Press, Bronx.
Felger, R. S. 2000. Flora of the Gran Desierto and Río Colorado Delta of Northwestern Mexico. University of Arizona Press, Tucson.
———, M. B. Johnson, and M. F. Wilson. 2001. The Trees of Sonora, Mexico. Oxford University Press, Oxford, U.K.
Finnegan, W. 2002. Leasing the rain. The New Yorker, April 8, 2002: 43–53.
Flora of Chile. http://www.efloras.org/flora_page.aspx?flora_id=60. [Sponsored by the Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Santiago.]
Flora of the Greater Antilles Newsletter. http://www.nybg.org/bsci/fga.
Forero, E. and A. H. Gentry. 1989. Lista anotada de las plantas del Departamento del Chocó, Colombia. Instituto Ciencias Naturales-Museo Historia Natural, Universidad Nacional de Colombia, Bogotá, Biblioteca Jose Jeronimo Triana No. 10: 1–142.
Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth-

Science Reviews 55: 73–106.
Freer, S. 2003. Linnaeus' Philosophia Botanica. Oxford University Press, Oxford, U.K.
Freire-Fierro, A. and D. A. Neill. 2002. La Botánica en el Nuevo Milenio. Memorias del Tercer Congreso Ecuatoriano de Botanica. FUNBOTANICA 4, Quito.
Frodin, D. G. 2001. Guide to the Standard Floras of the World. Cambridge University Press, Cambridge, U.K.
Funk, V. A., A. K. Sakai, and K. Richardson (Organizers). 2002. Symposium: Biodiversity, Systematics, and Conservation. Syst. Biol. 51: 235–363.
Garden (The Garden Society, New York Botanical Garden). 1982. Special Issue: The Amazon Basin. Vol. 6, January/February, 1982.
Geist, H. J. and E. F. Lambin. 2002. Proximate causes and underlying driving forces of tropical deforestation. BioScience 52: 143–150.
Gentry, A. H. 1982. Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Missouri Bot. Gard. 69: 577–593.
——— and J. Lopez-Parodi. 1980. Deforestation and increased flooding of the upper Amazon. Science 210: 1354–1356.
Gernandt, D. S., G. Geada Lopez, S. Ortiz García, and A. Liston. 2005. Phylogeny and classification of *Pinus*. Taxon 54: 29–42.
Gewin, V. 2002. All living things, online. Nature 418: 362–363. [Can taxonomy shed its dusty image and reinvent itself as a vibrant discipline for the internet age?]
Giles, J. 2005. Millennium group nails down the financial value of ecosystems. Nature 434: 547.
Global Biodiversity Information Facility. http://www.gbif.org.
Global Land Cover Network Bulletin. November-December 2006. http://www.glcn.org/news. [Download No. 9 November-December 2006 newsletter.]
Godfray, H. C. J. 2002. Towards taxonomy's "glorious revolution." Nature 420: 461. [See also Nature 417: 17–19, 2002; Nature 419: 337, 2002.]
Goldblatt, P. (ed.). 1993. Biological Relationships between Africa and South America. Yale University Press, New Haven, CT.
Gómez-Pompa, A., C. Vázquez, and S. Guevara. 1972. The tropical rain forest: A nonrenewable resource. Science 177: 762–765.
Gorman, J. R. (ed.). 1973. Paraguay: Ecological Essays. Academy of the Arts and Sciences of the Americas, Miami.
Gottgens, J. F., R. H. Fortney, J. Meyer, J. E. Penney, and B. E. Rood. 1998. The case of the Paraguay-Paraná waterway ("Hidrovia") and its impact on the Pantanal of Brazil: A summary report to the Society of Wetland Scientists. Wetlands Bull. 15: 12–18.
Goulding, M., R. Barthem, and E. Ferreira. 2003. The Smithsonian Atlas of the Amazon. Smithsonian Institution Press, Washington, D.C.
Graham, A. 1999. Late Cretaceous and Cenozoic History of North American Vegetation (north of Mexico). Oxford University Press, Oxford, U.K.
Grayum, M. H. 1992. Comparative External Pollen Ultrastructure of the Araceae and Putatively Related Taxa. Monogr. Syst. Bot. Missouri Bot. Gard. 43.
Groombridge, B. and M. D. Jenkins. 2002. World Atlas of Biodiversity: Earth's Living Resources in the 21st Century. University of California Press, Berkeley.
Guillaument, J.-L., M. Belin, and H. Puig (eds.). 1996. Phytogéographie Tropical: Réalités et Perspectives. Orstom Éditions, Paris.
Halling, R. E. and G. M. Mueller. 2005. Common Mushrooms of the Talamanca Mountains, Costa Rica. New York Botanical Garden Press, Bronx.
Hammond, D. (ed.). 2005. Tropical Rainforests of the Guianan Shield. Oxford University Press, Oxford, U.K.
Harley, M. M., U. Song, and H. I. Banks. 2005. Pollen morphology and systematics of Burseraceae. Grana 44: 282–299.
Harris, R. 2005a. Attacks on taxonomy. Amer. Sci. 93: 311–312.
———. 2005b. To be free, or not to be, what is the commercial value of biodiversity data? Amer. Sci. 93: 505–506.
Harvard University (Gray) Herbarium. http://www.huh.harvard.edu. [Collections databases, Index of New World Plant Names.]
Havstad, K. M., L. F. Huenneke, and W. H. Schlesinger (eds.). 2006. Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site. Oxford University Press, Oxford, U.K.
Heckadon-Moreno, S. 1998. Naturalist del Istmo de Panamá. Instituto Smithsonian de Investigaciones Tropicales, Balboa, Panamá.
Henderson, A. 1995. The Palms of the Amazon. Oxford University Press, Oxford, U.K.
———, G. Galeano, and R. Bernal. 1995. Field Guide to the Palms of the Americas. Princeton University Press, Princeton, NJ.
Hopkin, M. 2005. Biodiversity and climate form focus of forest canopy plan. Nature 436: 452.
Hopkins, M. J. G. 2007. Modelling the known and unknown plant biodiversity of the Amazon Basin. J. Biogeogr. 34: 1400–1411.
Huber, O. 1982. Significance of savanna vegetation in the Amazon territory of Venezuela. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 221–244.
Husted, R. 2001. Letters: But maybe counting is the easiest part. Science 294: 1834.
Innes, J. L. and K. B. H. Er. 2002. Questionable utility of the frontier forest concept. BioScience 52: 1095–1109.
Instituto Nacional de Estandistica, Geografía e Informática. 1982. Carta de México. Topográfica 1: 250,000.
International Plant Names Index. http://www.ipni.org.
International Union for Conservation of Nature and Natural Resources Red List of Threatened Species. http://www.

iucnredlist.org.
Iremonger, S. 2002. A Guide to the Plants in the Blue Mountains of Jamaica. University of the West Indies Press, Kingston, Jamaica.
Janzen, D. H. 1974. Swollen-thorn Acacias of Central America. Smithsonian Contributions to Botany, No. 13. Smithsonian Institution Press, Washington, D.C.
——— and R. Liesner. 1980. Annotated check-list of plants of lowland Guanacaste Province, Costa Rica, exclusive of grasses and non-vascular cryptogams. Brenesia 18: 15–90.
Jardim, A., T. Killeen, and A. Fuentes. 2004. Guía de los Árboles y Arbustos del Bosque Seco Chiquitano, Bolivia. Missouri Botanical Garden Press, St. Louis.
Jardim Botânico do Rio de Janeiro. 2000. CD-ROM, Mata Atlântica—500 Anos. Jardim Botânico do Rio de Janeiro/ Estação da Arte, Rio de Janeiro.
Jawad, J. T., D. S. Seigler, and J. E. Ebinger. 2000. A systematic treatment of *Acacia coulteri* (Fabaceae, Mimosoideae) and similar species in the New World. Ann. Missouri Bot. Gard. 87: 528–548.
Judziewicz, E. J., L. G. Clark, X. Londoño, and M. J. Stern. 1998. American Bamboos. Smithsonian Institution Press, Washington, D.C.
Kaiser, J. 2002. Satellites spy more forest than expected. Science 297: 919.
Kalliola, R., M. Puhakka, and W. Danjoy (eds.). 1993. Amazonia Peruana: Vegetación Húmeda Tropical en el Llano Subandino. Proyecto Amazonia, Universidad de Turku, Turku, Finland; y Officina Nacional de Evaluación de Recursos Naturales, Lima.
Kareiva, P. and M. Marvier. 2003. Conserving biodiversity coldspots. Amer. Sci. 91: 344–351.
Kate, K. T. 2002. Science and the convention on biological diversity. Science 295: 2371–2372.
Keating, R. C., V. C. Hollowell, and T. B. Croat (eds.). 2005. Festschrift for William G. D'Arcy: The Legacy of a Taxonomist. Monogr. Syst. Bot. Missouri Bot. Gard. 104.
Kelloff, C. L. and V. A. Funk. 2004. Phytogeography of the Kaieteur Falls, Potaro Plateau, Guyana: Floral distributions and affinities. J. Biogeogr. 31: 501–513.
Kelly, D. L. et al. (+5 authors). 1988. Jamaican limestone forests: Floristics, structure and environment of three examples along a rainfall gradient. J. Trop. Ecol. 4: 121–156.
Kenicer, G. J., T. Kajita, R. T. Pennington, and J. Murata. 2005. Systematics and biogeography of *Lathyrus* (Leguminosae) based on internal transcribed spacer and cpDNA sequence data. Amer. J. Bot. 92: 1199–1209.
Kier, G. et al. (+ 6 authors). 2005. Global patterns of plant diversity and floristic knowledge. J. Biogeogr. 32: 1107–1116.
Kiesling, R. 1994 et seq. Flora de San Juan, República Argentina. Vol. 1 et seq. Missouri Botanical Garden Press, St. Louis.
Klucking, E. P. 1986 et seq. Leaf Venation Patterns. Vol. 1. Annonaceae. J. Cramer, Berlin.
Körner, C. 1999. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Springer Verlag, Berlin.
——— and J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31: 713–732.
Kreft, H. and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. Proc. Natl. Acad. Sci. U.S.A. 104: 5925–5930.
Kricher, J. 2002. Galápagos. Smithsonian Natural History Series. Smithsonian Institution Press, Washington, D.C.
Küchler, A. W. (ed.). 1970. International Bibliography of Vegetation Maps: Vol. 4, Africa, South America and World Maps. University of Kansas Publications, Library Series 36. University of Kansas, Lawrence.
Lack, H. W. 2004. The botanical field notes prepared by Humboldt and Bonpland in tropical America. Taxon 53: 501–510.
Lal, R., J. M. Kimble, and B. A. Stewart (eds.). 2000. Global Climate Change and Tropical Ecosystems. Lewis Publishers and CRC Press, Boca Raton, FL. [Tropical ecosystems as a carbon sink.]
Lamb, D., P. D. Erskine, and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. Science 310: 1628–1632.
Larson, E. J. 2001. Evolution's Workshop: God and Science on the Galapagos Islands. Basin Books, New York. [See review, J. Cain, Nature 412, 23 August 2001, pp. 767–768.]
Lauer, W. and D. Rafiqpoor. 2002. Die Klimate der Erde: Eine Klassification auf der Grundlage de Ökophysiologischen Merkmale der Realen Vegetation. Franz Steiner Verlag, Stuttgart.
Laurance, W. F., A. Albernaz, P. Fearnside, H. L. Vasconcelos, and L. Ferreira. 2004. Deforestation in Amazonia. Science 304: 1109–1111.
Lawlor, G. and D. Lawlor. 2002. Walter's Vegetation of the Earth. 4th revised ed., translated from the German 7th ed. Springer Verlag, Berlin.
Leith, H. and M. J. A. Werger (eds.). 1989. Tropical Rain Forest Ecosystems. Ecosystems of the World 14B. Elsevier Science Publishers, Amsterdam.
Lellinger, D. B. 1989. Ferns and Fern-Allies of Costa Rica, Panama, and the Chocó. (Part 1, Psilotaceae through Dicksoniaceae). Missouri Botanical Garden Press, St. Louis.
Lentz, D. L. and R. Dickau. 2005. Seeds of Central America and southern Mexico: The economic species. Mem. New York Bot. Gard. 91.
Levin, P. S. and D. A. Levin. 2002. The real biodiversity crisis. Amer. Sci. 90: 6–8.
Levin, S. A. (ed.). 2000. Encyclopedia of Biodiversity. Academic Press, London. [5-volume set with online version.]
Lewin, R. 1987. Recount on Amazon trees. Science 239: 563.
Lewis, G., B. Schrire, B. MacKinder, and M. Lock (eds.). 2005. Legumes of the World. Royal Botanic Gardens, Kew, Richmond, U.K.
Linares-Palomino, R., R. T. Pennington, and S. Bridgewater.

2003. The phytogeography of the seasonally dry tropical forests in equatorial Pacific South America. Candollea 58: 473–499. [Ecuador, Peru.]

Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. Biogeography. 3rd ed. Sinauer Associates, Sunderland, MA.

López, R. P. 2003. Phytogeographical relations of the Andean dry valleys of Bolivia. J. Biogeogr. 30: 1659–1668.

Lorence, D. H. 1999. A Nomenclator of Mexican and Central American Rubiaceae. Monogr. Syst. Bot. Missouri Bot. Gard. 73.

Lyonia, Journal of Ecology and Application. 2005–2006. Proceedings of the II International Dry Forest Congress, III Congress of Conservation of Biodiversity in the Andes and Amazon, and VI Ecuadorian Botanical Congress. Vol. 8 (2), 2005. Dry Forest Biodiversity and Conservation 1: Biodiversity; Vol. 9 (1), 2006. Biodiversity and Cultural Diversity in the Andes and Amazon 1: Biodiversity; Vol. 9 (2), Dry Forest Biodiversity and Conservation 2: Propagation and Conservation Strategies; Vol. 10 (1), Biodiversity and Cultural Diversity in the Andes and Amazon 2: Forest Conservation Strategies; Vol. 10 (2), Biodiversity and Cultural Diversity in the Andes and Amazon, Dry Forest Conservation, Ethnobotany and Forest Use.

Madsen, J. E., R. Mix, and H. Balslev. 2001. Flora of Puna Island: Plant Resources on a Neotropical Island. Aarhus University Press, Aarhus, Denmark. [An island in the Gulf of Guayaquil, Ecuador.]

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford, U.K.

Margolis, M. 1995. Treasuring the pantanal. Int. Wildlife 25: 12–21.

Marris, E. 2005. The forgotten ecosystem. Nature 437: 944–945. [Everyone knows about the Amazon rain forest, but Brazil's tropical savanna is arguably under greater threat. Emma Marris visits a testing ground for future conservation strategies.]

Marticorena, C. 1992. Bibliografía Botánica Taxonómica de Chile. Monogr. Syst. Bot. Missouri Bot. Gard. 41.

———, T. F. Stuessy, and C. M. Baeza. 1998. Catalogue of the Vascular Flora of the Robinson Crusoe or Juan Fernández Islands, Chile. Gayana, Bot. 55: 187–211.

Mauseth, J. D., R. Kiesling, and C. Ostolaza. 2002. Cactus Odyssey: Journeys in the Wilds of Bolivia, Peru, and Argentina. Timber Press, Portland.

McCarter, J., G. Boge, and G. Darlow. 2001. Safeguarding the world's natural treasures. Science 294: 2099–2101.

McClaran, M. P. and T. R. Van Devender (eds.). 1996. The Desert Grassland. University of Arizona Press, Tucson.

McDowell, N. 2002. Ecological footprint forecasts face skeptical challenge. Nature 419: 656.

McKinney, M. L. and J. A. Drake (eds.). 1998. Biodiversity Dynamics. Columbia University Press, New York.

McNulty, E. 2003. This time in Ecuador. Missouri Bot. Gard. Bull. May/June: 26–27. [Profiles curator David Neill and the Missouri Botanical Garden's projects in Ecuador.]

McPherson, G. R. 1997. Ecology and Management of North American Savannas. University of Arizona Press, Tucson.

McVaugh, R. (W. R. Anderson, gen. ed.). 1983 et seq. Flora Novo-Galiciana. University of Michigan Press, Ann Arbor.

———. 2000. Botanical Results of the Sessé & Mociño Expedition (1787–1803). VII. A Guide to Relevant Scientific Names of Plants. Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh.

Meggers, B. 1995. Amazonia: Man and Culture in a Counterfeit Paradise. Revised edition. Smithsonian Institution Press, Washington, D.C.

Michener, W. K. et al. (+ 6 authors). 2001. Defining and unraveling biocomplexity. BioScience 51: 1018–1023.

Missouri Botanical Garden Mesoamerica Project. http://www.mobot.org/mobot/research/mesoamericaprojects.shtml. [See also http://www.mobot.org/mobot/research/gallery/lagallery1.shtml for a Latin American plant image gallery.]

Mittermeier, R. A., I. G. Cámara, M. T. J. Pádua, and J. Blanck. 1990. Conservation in the pantanal of Brazil. Orynx 24: 103–112.

Moffat, A. S. 1996. Biogeographers take a new view of the ancient Andes. Science 272: 1420–1421.

———. 2002. South American landscapes: Ancient and modern. Science 296: 1959–1961.

Monbiot, G. 2005. Time to speak up for climate-change science. Nature 434: 559.

Montúfar-López, A. 1985. Lluvia de Polen Actual en Bromelias, Musgos y Suelo Superficial en los Alrededores de Santa Marta, Ocozocoautla, Chiapas. Estudios Palinológicos y Paleoethnobotánicos. Instituto Nacional de Antropología e Historia, México, D.F.

Mooney, H., A. Cropper, and W. Reid. 2005. Confronting the human dilemma, how can ecosystems provide sustainable services to benefit society? Nature 434: 561–562.

Moore, D. M. 1983. Flora of Tierra del Fuego. A. Nelson, London; Missouri Botanical Garden, St. Louis.

Moore, P. D. 2001. The guts of seed dispersal. Nature 414: 406–407. [Some plants have evolved delicious fruits to entice animals and birds into dispersing their seeds. But the seeds' dormancy and germinability are affected by which bird they pass through.]

———. 2003. Palms in motion. Nature 426: 26–27. [Palm seed dispersal by tapirs; for article see Fragoso et al., 2003, Ecology 84: 1998–2006.]

Morehead, A. 1969. Darwin and the Beagle. Harper & Row, New York.

Mullen, C. K. 1999. Flowering Plants of the Galapagos. Comstock Publishing Association, Cornell University Press, Ithaca, NY.

Mumby, P. J. et al. (+ 11 authors). 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427: 533–536.

Mycokey Web site. Key to the fungi of Ecuador. http://www.mycokey.com/Ecuador.html.

Myers, N. 1981. The hamburger connection: How Central America's forest became North America's hamburgers. Ambio 10: 3–8.

——— (ed.). 1992. Tropical Forests and Climate. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Nathan, R. 2006. Long-distance dispersal of plants. Science 313: 786–788.

Nature Conservancy. 2007. Cerrado: Global grassland perspective. The Nature Conservancy, Missouri Update, Fall 2007: 7.

Newman, A. 2002. Tropical Rainforest: Our Most Valuable and Endangered Habitat with a Blueprint for Its Survival into the Third Millennium. Checkmark Books, New York.

New York Botanical Garden International Plant Science Center Web site. http://sciweb.nybg.org/Science2/. [Bibliography of American botanical literature (39,000 entries), 85,000 images of type specimens.]

New York Botanical Garden Vascular Plant Types Catalog. http://www.nybg.org/bsci/hcol/vasc/.

Nixon, K. C. and J. M. Poole. 2003. Revision of the Mexican and Guatemalan species of *Platanus* (Platanaceae). Lundellia 6: 103–137.

Nogueira Ferraz, E. M., E. de Lima Araújo, and S. Izídio da Silva. 2004. Floristic similarities between lowland and montane areas of Atlantic coastal forest in northeastern Brazil. Pl. Ecol. 174: 59–70.

Novotny, V. et al. (+ 6 authors). 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313: 1115–1118. [These findings suggest that the latitudinal gradient in insect species richness could be a direct function of plant diversity, which increased sevenfold from our temperate to tropical study sites.]

O'Brian, T. G. and M. F. Kinnaird. 2003. Caffeine and conservation. Science 300: 587. [See also Letters-Response, Science 303 (2004): 625–626; Footnote 10, Chapter 1.]

Ocean Oasis Web site. http://www.oceanoasis.org. [Field guide of plants on the Sea of Cortez and the Baja California Desert. Site created by the San Diego Natural History Museum in conjunction with the film *Ocean Oasis*.]

Office of Geography, Department of the Interior. 1956. Official Standard Names Approved by the U.S. Board on Geographic Names, Mexico. Washington, D.C.

Oliveira-Babinski, M. E. C. B. and D. Mussa. 1986. Problemas de terminologia morfológica e anatômica em lingua portuguesa e de nomenclatura binomial de fitofósseis e vegetais atuais—Relatório de debates. Bol. IS-USP 17: 141–147.

Olsen, D. M. et al. (+ 17 authors). 2001. Terrestrial ecoregions of the world: A new map of life on Earth. BioScience 51: 933–938.

O'Riordan, T. and S. Stoll-Kleemann (eds.). 2002. Biodiversity, Sustainability and Human Communities: Protecting Beyond the Protected. Cambridge University Press, Cambridge, U.K.

Organization for Tropical Studies. http://www.ots.ac.cr. [Tropical biology database.]

Ozanne, C. M. P. et al. (+ 12 authors). 2003. Biodiversity meets the atmosphere: A global view of forest canopies. Science 301: 183–186.

Pachepsky, E., J. W. Crawford, J. L. Bown, and G. Squire. 2001. Towards a general theory of biodiversity. Nature 410: 923–926.

Park, C. C. 1992. Tropical Rainforests. Routledge, New York.

Patterson, D. J. 2003. Progressing towards a biological names register, how taxonomy could harness the indexing and organizational powers of the Internet. Nature 422: 661.

Paul, E. 2002. The riches of biological research—An elusive number? BioScience 52: 1080.

Pennington, R. T., G. P. Lewis, and J. A. Ratter. 2006. Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation. CRC Press, Taylor and Francis Group, Boca Raton, FL.

Pennington, T. D. and J. Saraukhán. 1998. Árboles Tropicales de México. 2nd ed. Universidad Nacional Autónoma de México, México, D.F.

Pennisi, E. 2000. Taxonomic revival. Science 289: 2306–2308. [By putting museum collections online and training students to be computer- and molecular biology–savvy, taxonomists hope their field will thrive in the new millennium. See also inset, Fossil databases move to the web, J. Kaiser.]

———. 2005. Sky-high experiments. Science 309: 1314–1315. [Global Canopy Research Network; using construction cranes to reach above towering tree tops, scientists are achieving a better overview of forest ecology and how trees contribute to global climate change.]

Peres, C. A., J. Barlow, and W. F. Laurance. 2006. Detecting anthropogenic disturbance in tropical forests. Trends Ecol. Evol. 21: 227–229.

Pimm, S. L. et al. (+ 32 authors). 2001. Can we defy nature's end? Science 293: 2207–2208.

Piñeiro, M. R., G. E. Giudice, and M. A. Morbelli. 2006. Spore morphology and sporoderm ultrastructure in *Adiantopsis* Fée (Pteridaceae-Pteridophyta) from Argentina. Grana 45: 101–108.

Plant Talk. http://www.plant-talk.org. [Saving the threatened plants and birds in the Andes of Ecuador; the Eden Project.]

Possingham, H. P. and K. A. Wilson. 2005. Turning up the heat on hotspots. Nature 436: 919–920.

Powledge, F. 2002. A look back at the International Biodiversity Observation Year. BioScience 52: 1070–1079.

———. 2003. Island biogeography's lasting impact. BioScience 53: 1032–1038.

Prance, G. T. (ed.). 1986. Tropical Rain Forests and the World Atmosphere. AAAS Selected Symposium 101. Westview Press, Boulder.

——— and T. S. Elias (eds.). 1977. Extinction Is Forever. New York Botanical Garden Press, Bronx.

——— and T. E. Lovejoy. 1985. Key Environments, Amazonia. Pergamon Press, Oxford, U.K.

Proches, S. et al. (+ 10 authors). 2005. Landscape corridors: Possible dangers? Science 310: 779–783. [Pathway for pathogens and invasives; see also response.]

Purcell, J., A. Brelsford, and M. Kessler. 2004. The world's highest forest. Amer. Sci. 92: 454–461. [*Polylepis* in the Bolivian Andes.]

Radford University. Major Biomes of the World: Temperate Broadleaf Deciduous Forest. http://www.runet.edu/~swoodwar/CLASSES/GEOG235/biomes/tbdf/tbdf.html.

Rangel, S. R., E. Rojas Zenteno, and M. Aguilar Enríquez. 2002. El género *Quercus* (Fagaceae) en el estado de México. Ann. Missouri Bot. Gard. 89: 551–593.

Rejmánek, M. and S. W. Brewer. 2001. Vegetative identification of tropical woody plants: State of the art and annotated bibliography. Biotropica 33: 214–228.

Ribeiro, J. E. et al. 1999. Flora da Reserva Ducke: Guía de Identificacão das Plantas Vasculares de uma Floresta de Terra-Firme na Amazônia Central. Instituto Nacional de Pesquisas da Amazonia (INPA) e Department for International Development (DFID), Manaus, Brazil.

Ribinoff, I. and E. G. Leigh Jr. 1990. Dealing with diversity: The Smithsonian Tropical Research Institute and tropical biology. Trends Ecol. Evol. 5: 115–118.

Ritter, N. P. 2004. Floristic composition and phytodiversity in the wetlands along the base of the Bolivian Andes. Rhodora 106: 1–32.

Rivas-Martínez, S. and O. Tovar. 1982. Vegetatio Andinae, I. Datos sobre las comunidades vegetales altoandinas de Los Andes Centrales del Perú. Lazaroa 4: 167–187.

Roberts, L. 1991. Ranking the rain forests. Science 251: 1559–1560.

Robichaux, R. H. (ed.). 1999. Ecology of Sonoran Desert Plants and Plant Communities. University of Arizona Press, Tucson.

——— and D. A. Yetman (eds.). 2000. The Tropical Deciduous Forest of Alamos: Biodiversity of a Threatened Ecosystem in Mexico. University of Arizona Press, Tucson.

Rogers, K. E. 2000. The Magnificent Mesquite. University of Texas Press, Austin.

Rottmann, J. 1988. Bosques de Chile/Chile's Woodlands. Ingeniería de Gestión (IGES), Santiago.

Royal Botanic Gardens, Kew. Kew Bibliographic Databases. http://kbd.kew.org/kbd/searchpage.do.

Royal Botanic Gardens, Kew. Kew Library main page. http://www.kew.org/library/index.html.

Royal Botanic Gardens, Kew. Electronic Plant Information Centre. http://epic.kew.org/index.htm.

Royal Botanic Gardens, Kew. Kew Herbarium Catalog. http://apps.kew.org/herbcat/navigator.do [Digitized specimen data and images from the Kew Herbarium.]

Rymer, R. 2004. Saving the music tree. Smithsonian 35: 52–63. [*Caesalpinia echinata*, pernambuco or Pau-brasil.]

Salati, E., H. O. R. Shubart, W. Junk, and A. D. de Oliveira. 1983. Amazônia: Desenvolvimento, Integracão e Ecología. Editora Brasiliense and Conselho Nacional de Desenvolvimento Científico e Technológico, Rio de Janeiro.

Santos-Granero, F. 1998. Selva Central: History, Economy, and Land Use in Peruvian Amazonia. Smithsonian Institution Press, Washington, D.C.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas. University of Chicago Press, Chicago.

Scarano, F. R. and A. C. Franco (eds.). 1998. Ecophysiological strategies of xerophytic and amphibious plants in the neotropics. Oecologia Brasiliensis (Programa de Pós Graduação em Ecología, Univ. Fed. Rio de Janeiro) 4: 1–233. [I. Estrutura, Funcionamento e Manejo de Ecosistémas Brasileiros; II. Tópicos de Tratamento de Datos Biológicos; III. Ecología de Praias Arenosas do Litoral Brasileiro.]

Schultes, R. E. and M. Jaramillo-Arango (translators, transcribed by J. Jaramillo-Arango). 1998. The Journals of Hipólito Ruiz, Spanish Botanist in Peru and Chile, 1777–1788. Timber Press, Portland.

——— and R. F. Raffauf. 1990. The Healing Forest: Medicinal and Toxic Plants of the Northwest Amazonia. Dioscorides Press, Portland.

Science. 2006. Migration and Dispersal. Special section, Science 313: 775–800. [See Introduction, Where to go, where to stop, A. Sugden and E. Pennisi, p. 775.]

Science Lives. http://www.geocities.com/sciencelives. [Articles on various science topics (e.g., tropical montane cloud forests, http://www.sciencelives.com/cloudforest1.htm).]

Shanley, P. and L. Luz. 2003. The impacts of forest degradation on medicinal plant use and implications for health care in eastern Amazonia. BioScience 53: 573–584.

Shouse, B. 2003. Old-growth forest spared for now. Science 299: 802. [Jeffrey pines in the San Pedro Mártir Mountains, Baja California.]

Siegert, F., G. Ruecker, A. Hinrichs, and A. A. Hoffman. 2001. Increased damage from fires in logged forests during droughts caused by El Niño. Nature 414: 437–440.

Sklenár, P., J. L. Luteyn, C. Ulloa Ulloa, P. M. Jørgensen, and M. O. Dillon. 2005. Flora Genérica de los Páramos: Guía Ilustrada de las Plantas Vasculares. Mem. New York Bot. Gard. 92.

Smith, A. 1990. Explorers of the Amazon. University of Chicago Press, Chicago.

Smith, N., S. A. Mori, A. Henderson, D. W. Stevenson, and S. V. Heald (eds). 2004. Flowering Plants of the Neotropics. Princeton University Press, Princeton, NJ.

Smithsonian Institution Digital Library. http://www.sil.si.edu/. [Includes Godman and Salvin's Biología Centrali-Americana; Scientific Identity, Portraits from the Dibner Library of the History of Science and Technology.]

Smithsonian Museum of Natural History Research and Col-

lections. http://www.mnh.si.edu/rc/. [See Botany, http://botany.si.edu; Paleobiology, http://paleobiology.si.edu/; Centres of Plant Diversity, http://botany.si.edu/projects/cpd/ (Mexico site MA1, Lacandón rain forest; Costa Rica site MA16, La Selva region; Caribbean Island site CB10, Blue Mountains of Jamaica; South America site SA39, Chocó of Colombia).]

Sociedad de Biologia de Chile. 1997. Program and Abstracts. II Southern Connection Congress, Southern Temperate Biota and Ecosystems, Past, Present and Future. Noticiero de Biología (Sociedad de Biología de Chile), Santiago.

Solbrig, O. T. and G. H. Orians. 1977. The adaptative characteristics of desert plants. Amer. Sci. 65: 412–421.

Sprichiger, R., P.-A. Loizeau, C. Latour, and G. Barriera. 1996. Tree species richness of a south-western Amazonian forest (Jenaro Herrera, Peru, 73°40'/4°54'S). Candollea 51: 559–577.

Stafford, P. and S. Knapp. 2006. Pollen morphology and systematics of the zygomorphic-flowered nightshades (Solanaceae; Salpiglossideae sensu D'Arcy, 1978 and Cestroideae sensu D'Arcy, 1991, pro parte): A review. Syst. Biodivers. 4: 173–201.

Standley, P. C. 1920 et seq. Trees and Shrubs of Mexico. Contr. U.S. Natl. Herb., Vol. 23 et seq.

Stearn, W. T. (ed.). 1968. Humboldt, Bonpland, Kunth and Tropical American Botany, A Miscellany on the "Nova Genera et Species Plantarum." J. Cramer Verlag, Stuttgart.

Stephens, J. L. 1850. Incidents of Travel in Central America, Chiapas, and Yucatan. Harper & Brothers, New York. [New edition, Karl Ackerman, 1996, Smithsonian Institution Press, Washington, D.C.]

Stevens, R. D. 2006. Historical processes enhance patterns of diversity along latitudinal gradients. Proc. Roy. Soc. London, Ser. B, Bibl. Sci. 273: 2283–2289.

Stocking, M. A. 2003. Tropical soils and food security: The next 50 years. Science 302: 1356–1359.

Stokstad, E. 2003. Unsuspected underground nitrates pose a puzzle for desert ecology. Science 302: 969. [See also pp. 1021–1024.]

———. 2005. Experimental drought predicts grim future for rainforest. Science 308: 346–347. [An extraordinary research effort in the Amazon starved a tropical forest of rain and provides a glimpse of the potential effects of climate change.]

Stolzenburg, W. 2001. Fire in the rain forest. Nat. Conservancy 51: 22–27.

Suarez, A. V. and N. D. Tsutsui. 2004. The value of museum collections for research and society. BioScience 54: 66–74.

Takeda, I. J. M. and P. Vitor Farago. 2001. Vegetação do Parque Estadual de Vila Velha, Guía de Campo. I. J. M. Takeda, Curitíba, Brazil.

Tellman, B. (ed.). 2002. Invasive Exotic Species in the Sonoran Region. University of Arizona Press, Tucson.

Tennesen, M. 2006. Uphill Battle. Smithsonian 37: 79–83. [Cloud forest shifts to higher elevations in the Andes with global warming; describes studies of Silman, Bush, Rapp, Peruvian colleagues Farfan, Garcia, and others at Lake Consuelo, Manú, Peru.]

Terborgh, J. 1992. Diversity and the Tropical Rain Forest. Scientific American Library Series 38. W. H. Freeman, New York.

Torres, L. 1998. Guía Práctica para las Plantas del Cerro Pataman, Município de Tangancicuaro y Los Reys, Estado de Michoacán, México. Field Museum, Chicago.

Trivedi, B. P. 2005. What's in a species name? More than $450,000. Science 307: 1399.

Tsuchiya, A. H. and C. R. Mario da Silva. 1997. Characterization and utilization of várzea and terra firme forests in the Amazon estuary. Bol. Mus. Paraense Emilio Goeldi, Ser. Bot., 13: 171–190.

Turner, I. M. 2001. The Ecology of Trees in the Tropical Rain Forest. Cambridge University Press, Cambridge, U.K.

Turner, R. M., J. E. Bowers, and T. L. Burgess. 1995. Sonoran Desert Plants: An Ecological Atlas. University of Arizona Press, Tucson.

UNEP–World Conservation Monitoring Center. http://www.unep-wcmc.org/protected_areas/data/nat2.htm. [Listing of protected areas of the world.]

Valiela, I., J. L. Bowen, and J. K. York. 2001. Mangrove forests: One of the world's threatened major tropical environments. BioScience 51: 807–815.

Valiente-Banuet, A., N. Flores-Hernández, M. Verdu, and P. Davila. 1998. The chaparral vegetation in Mexico under non-Mediterranean climate: The convergence and Madrean-Tethyan hypotheses reconsidered. Amer. J. Bot. 85: 1398–1408.

Válka Alves, R., L. Cardin, and M. S. Kropf. 2007. Angiosperm disjunction "campos rupestres–restingas": A re-evaluation. Acta Bot. Brasil. 21: 675–685.

Van't Klooster, C., J. C. Lindeman, and M. J. Jansen-Jacobs. 2003. Index of vernacular plant names of Suriname. J. Pl. Taxon. Pl. Geogr. (Suppl.) 15: 1–322.

Vargas Calderón, C. 1994. Flora del Sur del Perú: Catalógo Sistemático del Herbário Vargas (CUZ). GTZ (Deutsche Gesellschaft für Technische Zusammenarbeit), Eschborn, Germany.

Vásquez Martínez, R. 1997. Flórula de las Reservas Biológicas de Iquitos, Perú. Monogr. Syst. Bot. Missouri Bot. Gard. 63.

——— and R. Rojas G. (eds.). 2004. Plantas de la Amazonía Peruana: Clave para Identificas las Familias de Gymnospermae y Angiospermae. Missouri Botanical Garden Press, St. Louis.

Vispo, C. and C. Knab-Vispo (eds.). 2003. Scientia Guaianae (a series on natural sciences of the Guayana region). 12 parts [as of 2003]. Ministerio Ciencia y Technología, Fundación Guayana, and Conservation International Venezuela, Caracas.

Wade, J. S. 1999. Brazilian Pantanal and Florida Everglades: A comparison of ecosystems, uses and management. Anais do II Simpósio sobre Recursos Naturalis e Socio-econômicos do Pantanal: Manejo e Conservação (1996, Corumbá, Brazil): 29–37.

Waldmann, G. and M. Stevens. 2001. Bibliography of the Natural History of the Lesser Antilles—With Particular Reference to the Terrestrial and Freshwater Environment (1900–2000). Acta Biologica Benrodis, Suppl., Band 8. Solingen, Germany.

Wallace, D. R. 1992. The Quetzal and the Macaw: The Story of Costa Rica's National Parks. Sierra Club Books, San Francisco.

Walters, T. and R. Osborne (eds.). 2004. Cycad Classification. Oxford University Press, Oxford, U.K.

Wanderley, M. G. L., G. J. Shepherd, and A. M. Giulietti (co-ordenadores). 2001 et seq. Flora Fanerogâmica do Estado de São Paulo. FAPSP: Editoria Hucitep, São Paulo.

Weaver, P. L. 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. Interciencia (Caracas) 16: 142–151.

Weber, A., W. Huber, A. Weissenhofer, N. Zamora, and G. Zimmermann (eds.). 2001. An Introductory Field Guide to the Flowering Plants of the Golfo Dulce Rain Forests, Costa Rica: Corcovado National Park and Piedras Blancas National Park. Oberösterreichisches Landesmuseum, Linz, Austria.

Weber, H. 1969. Zur Natürlichen vegetationsgliederung von Südamerika. *In:* E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli (eds.), Biogeography and Ecology in South America, Vol. 2. Dr. W. Junk Publishers, The Hague. pp. 475–518.

Webster, F. and M. S. Webster. 2001. Road to El Cielo: Mexico's Forest in the Clouds. University of Texas Press, Austin.

Webster, G. L. and C. J. Bahre (eds.). 2001. Changing Life of La Frontera: Observations on Vegetation in the United States/Mexico Borderlands. University of New Mexico Press, Albuquerque.

Wheeler, Q. D., P. H. Raven, and E. O. Wilson. 2004. Taxonomy: Impediment or expedient? Science 303: 285. [See also p. 310.]

Whitfield, J. 2002. Half the Earth still wild. Nature 420: IX.

Whitfield, S. M. et al. (+ 7 authors). 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. Proc. Natl. Acad. Sci. U.S.A. 104: 8352–8356.

Whitmore, T. C. 1990. An Introduction to Tropical Rain Forests. Oxford University Press, Oxford, U.K.

Wilbur, R. L. 1986 et seq. The vascular flora of La Selva Biological Station. Introduction. Selbyana 9: 191.

Wilson, D. E. and A. Sandovol. 1996. Manu: The Biodiversity of Southeastern Peru. Smithsonian Institution Press, Washington, D.C.

Woodward, L. L. and R. L. Woodward. 1985. Trudi Blom and the Lacandón rain forest. Environmen. Rev. 9: 226–236.

World Information Network on Biodiversity. http://www.conabio.gob.mx/remib_ingles/doctos/remib_ing.html.

Young, K. R. and B. Léon. 1989. Pteridophyte species diversity in the central Peruvian Amazon: Importance of edaphic specialization. Brittonia 41: 388–395.

Zanoni, T. A., M. M. Mejía, J. D. Pimentel, and R. G. García. 1990. La flora y la vegetación de Los Haitises, República Dominicana. Moscosoa 6: 46–95.

Zuloaga, F. O., O. Morrone, and M. J. Belgrano (eds.). 2008. Catálogo de las Plantas Vasculares del Cono Sur (Argentina, Sur du Brasil, Chile, Paraguay y Uruguay). 3 Vols. Missouri Botanical Garden Press, St. Louis.

SECTION II

DATABASE

Late Cretaceous and Cenozoic Floras and Terrestrial Paleoenvironments

Nullius in Verba **(Take no man's word for it)**

Motto on the coat of arms of the Royal Society (London) granted by Charles II,

September 17, 1662

Information on the history of Latin American vegetation is meager in relation to the size and diversity of the area and especially so for plant megafossils (Fig. 4.1). The region has exchanged plants with Australasia via Antarctica; northern North America over the Panama and Antillean land bridges; temperate Europe and Asia across the North Atlantic and Bering land bridges; and with Africa by overland migration in the Cretaceous and early Paleogene and later by long-distance dispersal. Both the modern vegetation and the fossil record document elements, progenitors, and descendants from all these regions in the modern Latin American plant formations.

It is also clear that factors determining climate are teleconnected (Chapter 7), so that processes originating in the middle and low latitudes are important in determining global temperatures and precipitation. Similarly, events operating elsewhere, as in the Indian Ocean (Walker circulation) and the North Atlantic Ocean (North Atlantic Deep Water Formation), influence climates toward the equator and in the southern polar regions (Markgraf, 2001). The present vegetation and environments of Latin America are part of a global system, and an integrated perspective is essential for conceptualizing their history.

Even though the data are limited, sufficient information does exist for parts of Latin America to construct probable scenarios of vegetation and climatic change, and to extrapolate these to lesser-known areas, times, ecosystems, and lineages. In Mexico, several studies have been made on Eocene through Pliocene floras, and on Late Glacial and Holocene assemblages of the northern deserts, the Transvolcanic Belt, and the Yucatán Peninsula–Maya lowlands. A few fossil floras are scattered through the Antilles, and there is a relatively good sequence of Cenozoic palynofloras from the canal region of Panama. In South America, there are extensive floras of Cretaceous and Cenozoic age from Argentina that have been studied for more than a century, and important assemblages from Brazil now being investigated. Quaternary vegetation and paleoenvironments are well known for the Sabana de Bogotá of Colombia and for southern Chile and adjacent Fuego–Patagonia, and projects are under way in the Andean highlands of Bolivia. The systems are complex, however, and the data are often contradictory to the extent of being described as "frustrating" in one recent review. Multidisciplinary, high-resolution, fully databased, broadly integrated, and sustained studies are required, but these are expensive and logistically difficult to bring about. Thus, it is noteworthy that many megafossil floras of critical age, located along biogeographically important pathways and containing records of phylogenetic and paleoecological interest, await revision nearly a century after the original studies (Graham, 2003).

Even so, new and unexpected discoveries are being made. Prior to the 1990s, Asian exotics were recognized in the Tertiary of northern North America, but it was not known how far south they extended. Then, fossils of the present-day Asian genus *Eucommia* were found in the Oligocene of central Mexico. An increasing number of other taxa are being reported from the past and present vegetation of Latin America, including

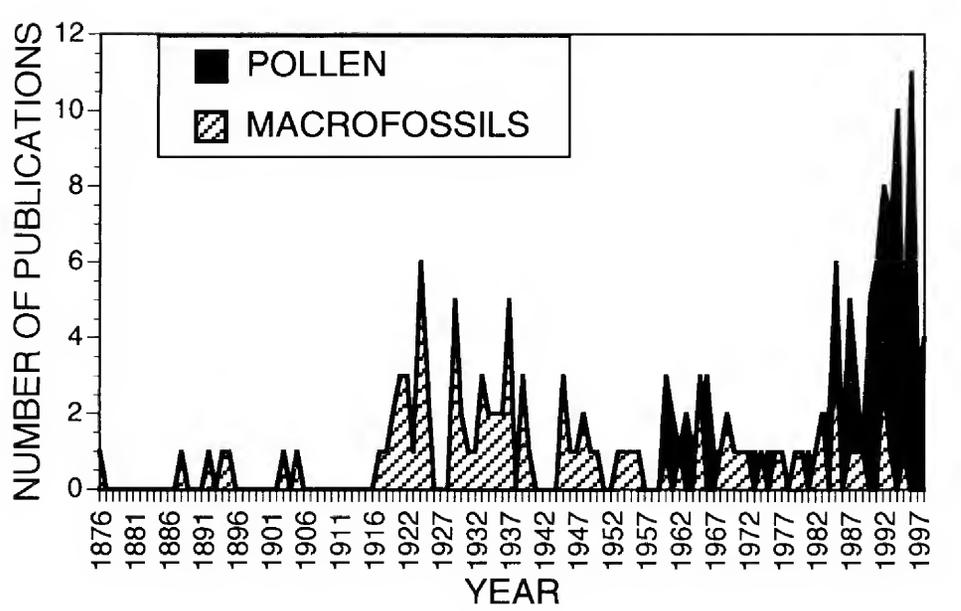


Figure 4.1. Publication activity in Neotropical paleobotany since 1876. From Burnham and Graham (1999). Used with permission of the Missouri Botanical Garden, St. Louis.

ones with African affinities, the Asian *Trigonobalanus* from the Andean forests of Colombia, the new family Ticodendraceae from the cloud forests of Central America and Mexico, and Welwitschiaceae from the Cretaceous of Brazil.

The Quaternary plant fossil record is providing evidence of how far south and to what extent climate-forcing mechanisms, initially identified from the high polar regions, extended across the middle latitudes, through the complex transitional zone of the Central Andes, and into southern South America. These mechanisms include the Milankovitch cycles, the Younger Dryas cold interval, Heinrich and D–O events, a mid-Holocene dry interval, the Medieval Warm Period, and the Little Ice Age. Terrestrial paleoenvironment reconstructions, based on paleobotany, are being compared with the marine record, based on oxygen isotopes and other techniques, regarding the unsettled issues of interhemispheric synchronizations and lag times. However, reading the accompanying plant fossil evidence assumes familiarity with some subtleties of paleobotanical nomenclature, and for the general reader and the nonspecialist, the names of modern taxa as applied to plant fossils require comment.

Cautionary notes and opinions 1 (Nomenclature):

In strata older than about the middle Eocene and in most deposits investigated for stratigraphic purposes, plant microfossils are named by an artificial system (e.g., *Monoporites annulatus*). Affinities or botanical relationships may be cited (e.g., Poaceae), or suggested by the name, but a wide range of often-unspecified intent is involved. For example, *Sparganiaceaepollenites* may mean the author believed the fossils were related to *Sparganium*. This would imply an awareness of the various biogeographical, paleoecological, stratigraphic, and phylogenetic implications of the report and that comparisons had been made using an extensive and vouchered reference collection. This is not always the case. A modern taxon may be cited primarily to augment the descriptions and illustrations of the specimen. Among the legions of examples, Doubinger

and Chotin (1975) cite the "affinités botaniques" of *Triorites minutipori* from the Paleocene of Chile as *Celtis* (Ulmaceae) and also as *Engelhardia* (Juglandaceae). In this case, the names were probably meant to convey a sense of the morphology (oblate shape, triporate), and not to suggest botanical affinities with two different families. The purposes of such comparisons vary widely, and they must be appraised before accepting and using biological affinities mentioned in the literature. A related cautionary note on identifications is given in Chapter 7, where early paleobotanical studies provide some relevant examples.

The composition of Late Cretaceous and Cenozoic floras in northern Latin America is given in Tables 4.1 (Mexico), 5.1 (the Antilles), and 6.1 (Central America). Late additions are mentioned in the text, and estimated ages or radiometric dates are given in Table 6.4. The same information is provided for South America in Tables 7.1 (Cretaceous and Paleogene), 7.2 (Neogene), and 7.6 (Quaternary), with dates for the floras in Table 7.3.

Chapter 4

MEXICO

LATE CRETACEOUS (83.5–65 MA)

Twenty-four fossil floras ranging in age from the Late Cretaceous (Campanian, 83.5 Ma) through the Holocene are used to trace the vegetation history of Mexico (Figs. 4.2, 4.3). At the beginning of the Late Cretaceous, land that would later become Baja California lay off the western coast of Mexico as a volcanic island arc. The La Misión and Rosario floras are two small megafossil assemblages of Campanian age on the west coast of northern Baja California that include gymnosperms identified as *Araucaria* and *Brachyphyllum* and the dicot cf. *Persea* (Lauraceae). Both floras were transported northward and represent the Late Cretaceous vegetation of mid-coastal Sonora (Axelrod, 1979). Inland, the fore-arc trench of the proto-Sierra Madre Occidental was still receiving sediments, but land was emerging from the accumulation of lava, ash, and other volcanic ejecta, and through uplift. The setting along this active continental margin was a relatively narrow coastal plain rising to low-elevation uplands. The vegetation on these uplands is unknown, although fossil plants of Maastrichtian age (71.3–65 Ma) are known from ~50 km south of Nogales in Sonora. They have not been studied in detail, and only *Obispocaulis myriophylloides* (stem) and *Tarahumara sophiae* (inflorescence),

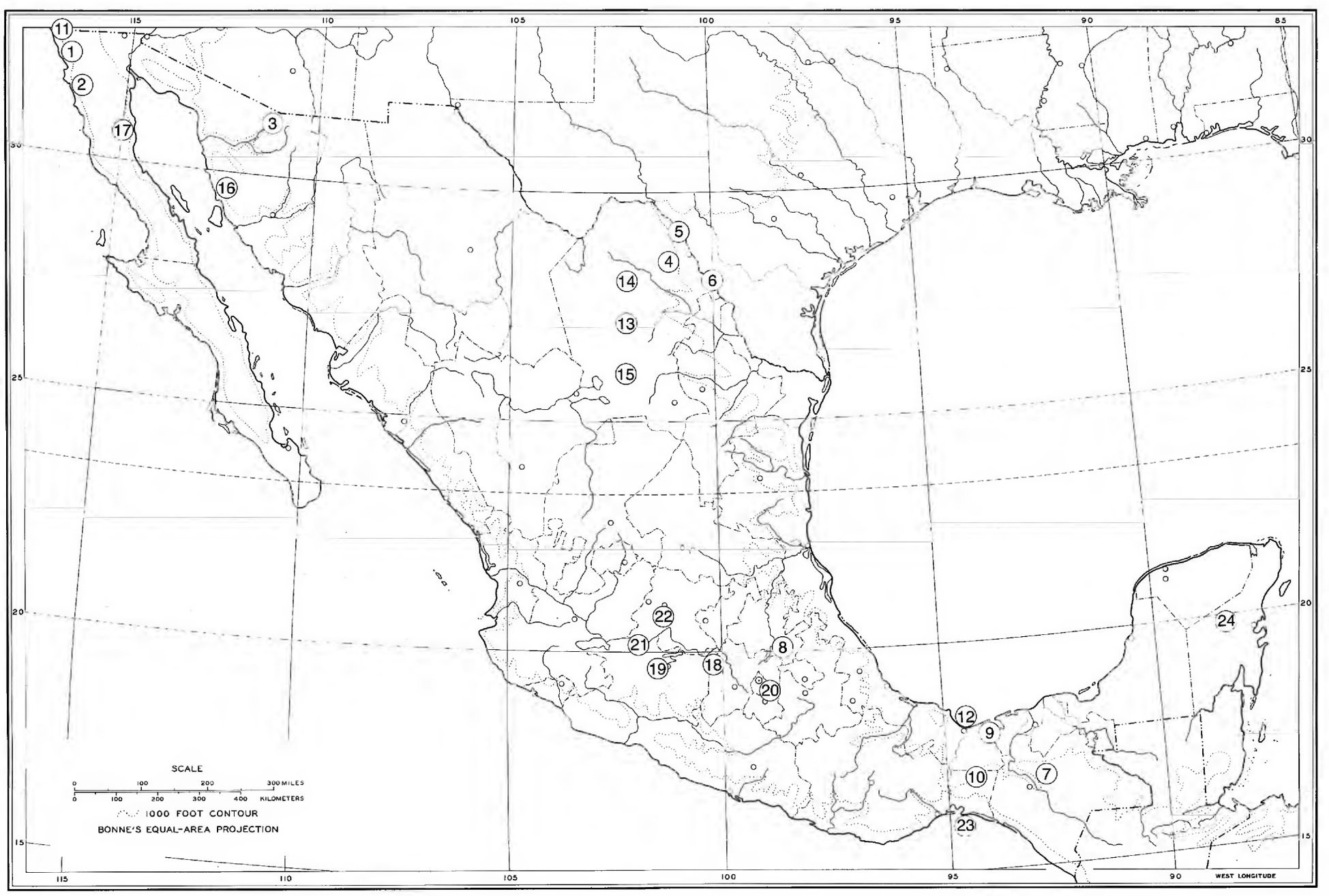


Figure 4.2. Location of fossil floras of Mexico mentioned in the text. Cretaceous: 1 = La Misión, 2 = Rosario, 3 = Huepac, 4 = Olmos, 5 = Piedras Negras; Eocene: 6 = Laredo–Burgos Basin; Oligo–Miocene: 7 = Simojovel–Ixtapa (El Bosque, La Trinidad, Simojovel [La Quinta flora]); Oligocene: 8 = Pie de Vaca; Miocene: 9 = San José de Carmen, 10 = Palomares, 11 = Mint Canyon; Pliocene: 12 = Paraje Solo; Quaternary: 13 = Cuatro Ciénegas, 14 = Alta Babicora, 15 = Cañon de la Fragua, Puerto de Ventanillas, Sierra de la Misericordia, 16 = Sierra Bacha, 17 = San Felipe, 18 = Iztapalapa–Valley of Mexico (Texcoco), 19 = Pátzcuaro, 20 = Puebla–Tlaxcala, 21 = Zacapú, 22 = Hoya San Nicolas de Parangueo, 23 = Tehuantepec, 24 = Cobá.

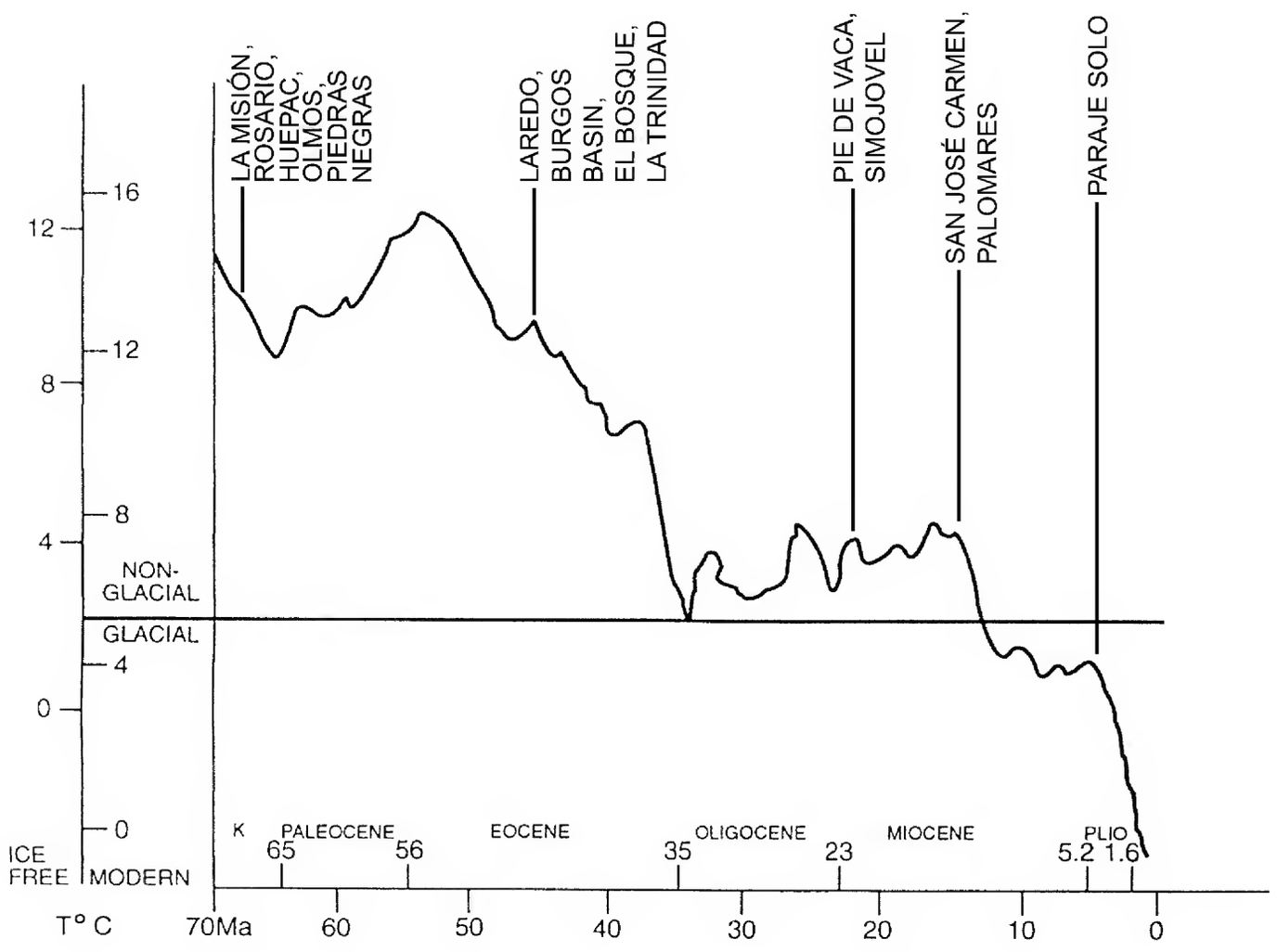


Figure 4.3. Global paleotemperature curve with Late Cretaceous and Tertiary floras of Mexico.

considered an aquatic angiosperm related to the Haloragaceae (tribe Myriophylleae), are described from the Huepac Chert member of the Tarahumara Formation (Hernández-Castillo & Cevallos-Ferriz, 1999; Figs. 4.2, 4.3; Table 4.1).

To the east, a more extensive flora is preserved in the Olmos Formation from the Sabinas region of Coahuila of late Campanian–early Maastrichtian age. The sediments are mostly marine, but the Olmos Formation includes organic lenses of plant debris that accumulated along the broader and gradually sloping eastern passive margin. The Olmos and other associated formations are the source of Mexico's limited commercial-grade coal. The sediments were deposited in a floodplain–delta environment just after the last marine regression from the region, and the fragmentary condition of many specimens indicates transport by rivers from the low-lying proto-Sierra Madre Oriental. Fossil plants described from the Olmos Formation include *Dorfiella auriculata*, an aquatic fern of unknown family affinity (Weber, 1976); *Salvinia coahuilensis* (Salviniaceae), a floating aquatic fern (Weber, 1973); the extinct conifers *Aachenia knoblochi* (ovuliferous cone scales and vegetative twigs; Weber, 1975), *Kobalostrobus olmosensis* (possibly the pollen cones of *Aachenia*; Serlin et al., 1980–1981), and *Raritania* and *Brachyphyllum* (mentioned by Serlin et al. [1980–1981] as being in the Olmos Formation); woods of *Podocarpoxylon* (Podocarpaceae) and *Taxodioxylon* (Taxodiaceae; Cevallos-Ferriz, 1992); and a dicotyledon wood of uncertain affinities (Cevallos-Ferriz & Weber, 1992). New woods described as including *Javelinoxylon weberi* (Malvaceae), *Quercinium centenoae* (Fagaceae), and *Sabinoxylon pasac* (fagaceous) are known from the Olmos Formation (Estrada-Ruiz et al., 2007). Fruits and infructescences (*Operculifructus lopenzii*, *O. latomatensis*, Alismatales?) have been described from the Cerro del Puebla Formation (late Campanian) of Coahuila by Estrada-Ruiz and Cevallos-Ferriz (2007), but the family affinities are unknown.

The gymnosperm and dicotyledon woods have poorly developed growth rings indicating moderate seasonality in temperature and rainfall (I: pp. 128–133), and some variation is attributed to habitat differences (coastal brackish swamps versus freshwater floodplains) rather than climate. This is consistent with a wealth of geological and paleontological information suggesting widespread continentality and equitable climates during the Maastrichtian (Chapter 2; I: ch. 5), including extensive Late Cretaceous (Aguja and Javelina formations) and Paleocene (Black Peaks Formation) woods from the adjacent Big Bend region of Texas (araucarioid, *Cupressioxylon*, cupressoid-podocarpoid types; Wheeler & Lehman, 2005). Context information further documents an equable, warm-temperate to subtropical climate (Fig. 4.3). Sedimentological evidence and isotopic analysis of carbonate nodules from paleosols (fossil soils) in Big Bend National Park indicate a warm climate drier (more seasonal) than that of the preceding Campanian, with a minimum MAT >15° C and possibly to 20°–25° C in the warmest intervals (I: p. 176). Although ~80 species occur in the flora (60 dicotyledons; Weber, 1972), only eight have been published. The Olmos–Big Bend flora is the largest Cretaceous plant megafossil assemblage in northern Latin America.

To the east, plant microfossils are known from Maastrichtian deposits near Piedras Negras ~125 km northeast of Sabinas. Some of the microfossils are Normapolles (Medus & Almeida-Leñero, 1982), a distinctive type of Late Cretaceous to early Oligocene pollen of unknown affinity, with complex and frequently protruding apertures (I: pp. 150–153; Fig. 4.4).

When the Cretaceous epicontinental sea divided North America into an eastern and western portion, the Normapolles defined the eastern province that extended into western Europe. The biological affinities of most spores and pollen from the Piedras Negras material cannot be established to family or genus because the sediments are too old and the preservation is marginal (Martínez-Hernández et al., 1980). To compare the flora with others, and to use the relevant literature, a formalized morphological system with illustrated and described type species is required. In the case of the Piedras Negras material, this standardized nomenclature is combined with some informal names (e.g., polen triporado). In addition to nomenclatural difficulties, deltaic sediments are notorious for differential preservation and for contamination by palynomorphs eroded from formations of different ages along the course of the rivers and deposited in a single depositional basin. Thus, characterization of the Cretaceous vegetation is not easy, but several aspects of the assemblages are still of interest. Six of the eight Olmos megafossils are gymnosperms, and five of these are conifers. This is consistent with the dominance of gymnosperms (with ferns and allied groups) in the preceding Triassic, Jurassic, and Early Cretaceous; their prominence in the Middle and Late Cretaceous at many sites; and the relatively open nature of the upland vegetation. Among the Piedras Negras microfossils, however, no winged conifer pollen is illustrated, suggesting that gymnosperms were not dominant throughout the region during the Maastrichtian, and that angiosperms had become a prominent component of the flora. There are more than 30 types of microfossils, excluding dinoflagellates, other algae, and fungi, indicating at least moderate angiosperm diversity and a more closed vegetation cover. The megafossils and microfossils collectively give an uncertain picture of the vegetation, and they record only a few taxa recognizable at the level of extant families or genera. Evidence from independent lines of inquiry is essential for even the provisional paleoenvironmental reconstructions mentioned earlier.

Among the family lineages reported for the Late Cretaceous of Mexico are Salviniaceae, Araucariaceae, Pinaceae, Podocarpaceae, Taxodiaceae, Betulaceae (*Carpinus* type), Juglandaceae (*Momipites* = *Alfaroa–Engelhardia–Oreomunnea* type, possibly some Normapolles), Lauraceae (*Persea* type), Myricaceae (*Myrica* type), and an unknown number of taxa from the undescribed material of the Olmos flora (Table 4.1; Appendices 2.1, 2.2).

PALEOCENE AND EOCENE (65–33.7 MA)

There are few Paleocene floras known from Mexico that are sufficiently diverse or well studied and dated to confidently record the presence of lineages or to make detailed paleoenvironmental reconstructions (see Ramírez-Arriaga et al., 2005; Paleogene, Puebla, Mexico). However, globally it is known that paleotemperatures rose after the asteroid impact and culminated in the LPTM or PETM (viz., the late Paleocene through early Eocene, [65–]55[–41] Ma; Schmitz et al., 2000; Kurtz et al., 2003; Utescher & Mosbrugger, 2007; Fig. 4.3), adding warmth to an already warm world (Pagani et al., 2006a). Surface temperatures in the high latitudes rose by ~5°–7° C over a period of <10 Kyr (Pagani et al., 2006b) to ~30 Kyr (Arctic surface water temperatures were at ~18° C), and were 6.7°–8.5° C warmer than at present (Bains et al., 2000; Brinkhuis et al., 2006; Moran et al., 2006; Sluijs et al., 2006; Stoll, 2006). In the equatorial regions, surface temperatures increased by ~5° C to a MAT of ~28° C, or at least as warm as present (Adams et al., 1990; Graham, 1994, 2000; Zachos et al., 2003), and the warmth was sustained for ~170 Kyr. Tropical conditions extended throughout the low to mid-elevations of Latin America, while cool temperate habitats were restricted to a very few sites at higher elevations. Increased carbon release (to 1125 ppmv; Lowenstein & Demicco, 2006) and an explosive input of the greenhouse gas methane (which oxidizes to CO_2) from vent complexes in the northeast Atlantic Ocean (Vøring and Møre basins, Norwegian Sea) are proposed as factors in the Eocene global warming event (Svensen et al., 2004). The methane release may have been triggered and sustained by a change to deep water convection in the North Pacific (Tripati & Elderfield, 2005; Nunes & Norris, 2006). Orbital forcing via the 405 Kyr and 100 Kyr eccentricity cycles (Lourens et al., 2005) and a bolide impact (Cramer & Kent, 2005) are other possible factors.

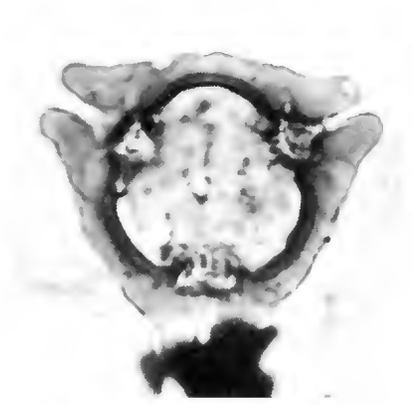


Figure 4.4. *Extratriporopollenites* sp., a Normapolles pollen from the base of the Late Cretaceous (Maastrichtian) Olmos Formation, Coahuila, Mexico. Reprinted from Medus and Almeida-Leñero (1982), with permission of Elsevier France.

Some indication of terrestrial Paleogene climatic trends in northern Baja California is provided by paleosol analysis. In the Paleocene and early Eocene, quartz-kaolinite mineralogy and cation-depleted chemistry of the soil indicate a humid, tropical climate (Peterson & Abbott, 1979). MAP is estimated at 1250–1900 mm, and MAT at 20°–25° C. Globally, the transition between the hothouse interval (warm, moist) and the icehouse interval (cooler, more seasonal) occurred toward the end of the early Eocene. Climates in Baja California became drier in the late Eocene as reflected by caliche horizons, vermiculite and smectite clays (implying drier conditions than the kaolinite clays of the early Eocene), and by conglomerate casts fractured from salt crystallization and transported 200–300 km by flash floods. MAP is estimated at 630 mm and is seasonal. Modern values are 250 mm and 16° C.

A study of modern palynomorph distribution in bottom sediments of southern Baja California was made by Cross et al. (1966), but to date there are no fossil assemblages from the area to which the data can be directly applied. There is one tantalizing but unsubstantiated report of Asteraceae pollen possibly in Paleocene–Eocene rocks in Baja California

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. Unless otherwise indicated, spellings, suggested biological affinities, families, and age assignments are according to the original authors. Unknowns and specimens designated by an informally applied artificial nomenclature (e.g., polen tricolparado) are not included. Unpublished studies are cited in the References but are not included in the Table. Spores and reproductive structures of fungi (e.g., cleistothecia), Pyrrophyta (dinoflagellates), and diatoms and other algae are often treated in separate publications, and only those cited in the references below are included here. Location by state is indicated under the column for Flora/Formation, and more specifically on Fig. 4.2. Refs. = references, as follows, Cretaceous (Campanian): 1 = Axelrod 1979; Cretaceous (Maastrichtian): 2 = Weber 1976, 3 = Weber 1973, 4 = Weber 1975, 5 = Cevallos-Ferriz 1992, 6 = Serlin et al. 1980–1981, 7 = Hernández-Castillo and Cevallos-Ferriz 1999, 8 = Medus and Almeida-Leñero 1982; Tertiary: 9 = Westgate and Gee 1990, 10 = Martínez-Hernández et al. 1980, 11 = Tomasini-Ortiz and Martínez-Hernández 1984, 12 = Magallón-Puebla and Cevallos-Ferriz 1993, 13 = Magallón-Puebla and Cevallos-Ferriz 1994a, 14 = Velasco de León and Cevallos-Ferriz 2000, 15 = Magallón-Puebla and Cevallos-Ferriz 1994b, 16 = Velasco de León et al. 1998, 17 = Ramírez and Cevallos-Ferriz 2002, 18 = Martínez-Hernández and Ramírez-Arriaga 1999, 19 = Miranda 1963, 20 = Langenheim et al. 1967, 21 = Graham 1999a, 22 = Fournier 1982, 23 = Martínez-Hernández 1992, 24 = Berry 1923, 25 = Axelrod 1979, 26 = Graham 1976a; Quaternary: 27 = Espinosa de G. Rul and Rzedowski 1966, 28 = Van Devender et al. 1990 (brackets indicate additional species from a: Van Devender 1990, b: Van Devender et al. 1994), 29 = Lozano-García et al. 2002 (Baja California), 30 = Meyer 1973 (Coahuila), 31 = Clisby and Sears 1955 (Basin of Mexico), 32 = Lozano-García and Ortega-Guerrero 1998 (Basin of Mexico), 33 = Straka and Ohngemach 1989 (Puebla–Tlaxcala), 34 = Almeida-Leñero et al. 1990 (Laguna de Quila, state of México), 35 = Arnauld et al. 1997 (Zacapú Basin, Michoacán), 36 = Watts and Bradbury 1982 (Pátzcuaro), 37 = Brown and Jacobs 1988 (Nayarit), 38 = Habib et al. 1970 (Tehuantepec), 39/40 = Leyden et al. 1994, Leyden 2002 (Yucatán, Guatemala); Undifferentiated: 41 = Felix and Nathorst 1893, 42 = Mullerried 1938. Brackets = present author's note or question.

Cretaceous (144–65 Ma; Campanian 83.5–71.3 Ma; Maastrichtian 71.3–65 Ma)

Megafossils

Taxon	Flora/Formation	Age	Ref.	Affinities
Araucaria	La Misión, B.C.	Campanian	1	Araucariaceae
	Rosario, B.C.	Campanian	1	Araucariaceae
Brachyphyllum	La Misión, B.C.	Campanian	1	Gymnospermae
cf. *Persea*	Rosario	Campanian	1	Lauraceae
Dorfiella auriculata	Olmos, Coahuila	Maastrichtian	2	Filicineae
Salvinia coahuilensis	Olmos, Coahuila	Maastrichtian	3	Salviniaceae
Aachenia knoblochi	Olmos, Coahuila	Maastrichtian	4	Pinaceae
Brachyphyllum	Olmos, Coahuila	Maastrichtian	5	Gymnospermae
Kobalostrobus olmosensis	Olmos, Coahuila	Maastrichtian	6	Coniferales
Podocarpoxylon	Olmos, Coahuila	Maastrichtian	5	Podocarpaceae
Raritania	Olmos, Coahuila	Maastrichtian	6	Gymnospermae
Taxodioxylon	Olmos, Coahuila	Maastrichtian	5	Taxodiaceae
Tarahumara sophiae–Obispocaulis myriophylloides	Tarahumara, Sonora	Maastrichtian–Campanian	7	aff. Haloragaceae aff. Haloragaceae

Microfossils

[8; Normapolles, *Aquilapollenites* (Triprojectacites) see I: p. 150; see also Martínez-Hernández et al., 1980; Upson, San Miguel/Olmos formations, Campanian/Maastrichtian, Coahuila]

Angiosperms (dicotyledons): *Alnipollenites trina* (Betulaceae), *Aquilapollenites*, *Carpinus subtriangula* (Betulaceae), *Complexiopollis abditus*, *Extratriporopollenites firmi(u)s*, *E.* cf. *longianulus*, *Ilexpollenites* (Aquifoliaceae), *Momipites tenuipolus* (~*Alfaroa–Engelhardia–Oreomunnea*, Juglandaceae), *Myrica annulites* (Myricaceae), *Nudopollis terminalis*, *N. thiergarti*, *Oculopollis baculotrudens*, *Plicapollis serta*, *Proteacidites* [Proteaceae?], *Pseudoplicapollis longiannulata*, *Pseudovacuopollis*, *Sinipites*, *Triatriopollenites excelsus*, *Triporopollenites bituitus*, *T. coryloides*, *Trudopollis* cf. *ana(o)culus*, *T.* cf. *meckeri*, *Vacuopollis*

Eocene (54.8–33.7 Ma; middle Eocene 49–41.3 Ma)

Microfossils

[9, Laredo Formation, Casa Blanca flora, middle Eocene (Claiborne), Webb County, Texas]

Ferns and allied groups: *Lygodiumsporites adriennis* (Pteridaceae, *Acrostichum*; or Schizaeaceae, *Lygodium*), *Pteris dentata* (Pteridaceae), *Selaginella* (Selaginellaceae). Angiosperms (monocotyledons): *Spinizonocolpites prominatus* (Palmae, *Nypa fruticans*). Angiosperms (dicotyledons): *Bombacacidites paulus* (probably Bombacaceae; possibly Sterculiaceae or Tiliaceae), *Lanagiopollis eocaenica* (Alangiaceae, *Alangium*), *Leea* (Leeaceae–Vitaceae), *Paraoreomunnea* (Juglandaceae, *Oreomunnea*, *Engelhardia* [or *Alfaroa*])

[10, Burgos Basin, Eocene, Colombia (Nuevo León), San Ignacio and Miguel Alemán (Tamaulipas); illustrated specimens only; see Ref. 10 for fungi, dinoflagellates, and other algae]

Algae: *Pediastrum*. Ferns and allied groups: *Appendicisporites*, *Camarozosporites*, *Cicatricosisporites* (Schizaeaceae), *Echinatisporis* cf. *aculeatus*, *Stereisporites crassiancoris*, *S. microgranulus-crassiexinus*, *Verrucatosporites* (verrucate monolete fern spores) *favus*, *V. megafavus*. Angiosperms (monocotyledons): *Liliacidites complexus*, *L. variegatus*, *Monocolpopollenites*, *Monocolporites*. Angiosperms (dicotyledons): *Alnipollenites*, *Bombacacidites claibornensis* (various spellings), *B. nacimientoensis* [probably Bombacaceae; possibly Sterculiaceae or Tiliaceae], *Chenopodipollis*, *Cupuliferoi*[*dae*]*pollenites*, *Extratriporopollenites*, *Ilexpollenites auriculoides* (Aquifoliaceae, *Ilex*), *Jussitriporites* (Onagraceae), *Momipites* [Juglandaceae], *Nudopollis terminalis*, *Platycarya swasticoida* (Juglandaceae), *Proxapertites*, *Sapotaceoidaepollenites*, *Symplocoipollenites*, *Tiliaepollenites vescipites*, *Tricolpites* cf. *variofoveatus*, *Triporopollenites*

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. *(Continued)*

[11, Huitiupan–El Bosque, Chiapas; Eocene section only, El Bosque, La Trinidad formations; see Ref. 11 for fungal spores; see also Ref. 11 under Oligocene for other age floras in the vicinity]

Ferns and allied groups: *Deltoidospora minor*, *Echinatisporites* (*Selaginella*). Gymnosperms [possibly reworked Cretaceous or older forms]: *Abietineaepollenites* (aff. cited as *Abies* [?]), *Cedripites* (aff. cited as *Cedrus* [?]), *Pristinuspollenites* (aff. cited as *Podocarpus* [?]); *Carollina torosus* [reworked?]. Angiosperms (monocotyledon): *Graminidites* (Gramineae). Angiosperms (dicotyledons): *Momipites corylipites* (Juglandaceae), *Nothofagus* (Fagaceae), *Parsonsidites conspicuous*, *Pellicieroipollis* (*Pelliceria*, Pelliceriaceae), *Tiliapollenites danei* [probably Sterculiaceae; possibly Tiliaceae or Bombacaceae], *Zonocostites* (*Rhizophora*, Rhizophoraceae)

Oligocene, Oligo–Miocene (33.7–23.8 Ma)

Megafossils

Taxon	Flora/Formation	Age	Ref.	Affinities
Geastrum tepexensis	Pie de Vaca, Puebla	Oligocene	12	Basidiomycete fungus
Cedrelospermum manchesteri	Pie de Vaca, Puebla	Oligocene	13	Ulmaceae (fruits)
Cercocarpus mixteca	Pie de Vaca, Puebla	Oligocene	14	*C. paucidentatus*, Rosaceae
Comocladia intermedia	Pie de Vaca, Puebla	Oligocene	17	Anacardiaceae
Eucommia constans	Pie de Vaca, Puebla	Oligocene	15	Eucommiaceae
Haplorhus medranoensis	Pie de Vaca, Puebla	Oligocene	17	Anacardiaceae
Karwinskia axamilpense	Pie de Vaca, Puebla	Oligocene	16	Rhamnaceae
Magdalenophyllum aequilaterum	Pie de Vaca, Puebla	Oligocene	13	Ulmaceae (leaves)
Pistacia marquezii	Pie de Vaca, Puebla	Oligocene	17	Anacardiaceae
Pseudosmodingium mirandae, *P. terrazasiae*	Pie de Vaca, Puebla	Oligocene	text	Anacardiaceae
Rhus toxicodendroides [*R. toxicodendron* in abstract]	Pie de Vaca, Puebla	Oligocene	17	Anacardiaceae
Rhus sp.	Pie de Vaca, Puebla	Oligocene	17	Anacardiaceae
Acacia sp.	formation unspecified, Simojovel, Chiapas	Oligo–Miocene	19	Leguminosae
Socratea brownii	Simojovel, Chiapas	Oligo–Miocene	Poinar, 2002	Palmae
Tapirira durhamii	formation unspecified, Simojovel, Chiapas	Oligo–Miocene	19	Leguminosae

Microfossils

[18, Pie de Vaca, Puebla, Oligocene, Tepexi de Rodríguez, Puebla]

Bryophytes: *Anthoceros*, *Sphagnum*. Ferns and allied groups: Cyatheaceae, Isoetaceae, *Laevigatosporites* [smooth monolete fern spores], *Lycopodium*, Polypodiaceae, Selaginellaceae. Gymnosperms: *Abies* (Pinaceae), *Cupressus–Juniperus–Taxodium* [often abbreviated c-t-t for Cupressaceae–Taxaceae–Taxodiaceae undifferentiated], *Dacri(y)dium* [Podocarpaceae; Indomalaysia, Chile], *Ephedra* (Ephedraceae), *Picea* (Pinaceae), *Pinus* (Pinaceae), *Podocarpus* (Pinaceae). Angiosperms (monocotyledons): Agavaceae, Gramineae, Liliaceae, Palmae, *Pandanus* [Pandanaceae; Old World tropics], Ponteder(i)aceae, *Sagittaria* (Alismataceae), *Typha* (Typhaceae). Angiosperms (dicotyledons): *Acacia* (Leguminosae), Acanthaceae, Anacardiaceae, *Armeria* (Plumbaginaceae), *Betula* (Betulaceae), Bignoniaceae, *Bombacacidites* (Bombacaceae), Boraginaceae, *Bursera* (Burseraceae), *Carya* (Juglandaceae), Caryophyllaceae, Leguminosae–Caesalpiniaceae, *Castanea* (Fagaceae), Chenopodiaceae–Amaranthaceae, Clethraceae, Compositae, *Corylus* (*–Ostrya–Carpinus*; Corylaceae), *Corsinipollenites* (Onagraceae), *Dorstenia* (Moraceae), *Drosera* (Droseraceae), *Eucommia* (Eucommiaceae), *Euphorbia* (Euphorbiaceae), Gesneriaceae, *Heliocarpus* (Tiliaceae), *Ilex* (Aquifoliaceae), *Juglans* (Juglandaceae), Labiatae, Leguminosae, *Liquidambar* (Hamamelidaceae), Malpighiaceae, Meliaceae, *Momipites coryloides* (Juglandaceae), *M. microcoryphaceous*, *M. triorbicularis*, *M. triradiatus*, Moraceae, Myrtaceae, *Platanus* (Platanaceae), Polygalaceae, Polygonaceae, Portulacaceae, *Pterocarya* (Juglandaceae), *Quercus* (Fagaceae), *Reevesia* [Sterculiaceae, Himalaya to Formosa], *Rhabdadenia* (Apocynaceae), Rosaceae, Rutaceae, Sapindaceae, Sapotaceae, Scrophulariaceae, Solanaceae, Tiliaceae, Ulmaceae, Urticaceae. Incertae sedis: *Aglaoredia*, *Catinipollis*, *Cretacaeiporites*, *Erdtmanipollis*, *Malvacipollis*, *Nuxpollenites*, *Rugubivesiculites*

[11, Huitiupan–El Bosque, Chiapas; Oligocene, Oligo–Miocene section, Rancho Berlin, La Quinta formations; *Hymanaea* amber spectrum; see also Ref. 11 under Eocene]

Ferns and allied groups: *Biretisporites* (*Hymenophyllum*, Hymenophyllaceae), *Cicatricosisporites* (Schizeaceae), *Deltoidospora minor* (Cyatheaceae), *Echinatisporites* (*Selaginella*, Selaginellaceae), *Laevigatosporites*, *Polypodiisporites* cf. *alienus*, *P.* cf. *favus*, *P.* cf. *megafavus*, *P.* cf. *tenellis*. Gymnosperms: *Abietineaepollenites* (*Abies* [?]), *Cedripites* (*Cedrus* [?]), *Cycadopites* (Cycadales), *Equisetosporites* (Ephedraceae), *Pristinuspollenites* (Podocarpaceae); *Carollina torosus* [reworked?]. Angiosperms (monocotyledons): *Arecipites* (Palmae), *Graminidites* (Gramineae), *Liliacidites variegatus* (Liliaceae). Angiosperms (dicotyledons): *Castaneapollenites*, *Echiperiporites*, *Momipites anellus* (*Alfaroa–Engelhardia–Oreomunnea*, Juglandaceae), *M. corylipites*, *M. microfoveolatus*, *Nothofagus* (Fagaceae), *Parsonsidites conspicuous*, *Pellicieroipollis* [*Pelliceria*, Pelliceriaceae/Theaceae], *Psilatricolporites crassus* [*Pelliceria*, Pelliceriaceae], *Tiliapollenites danei* [probably Sterculiaceae; possibly Tiliaceae or Bombacaceae], *Zonocostites* (*Rhizophora*, Rhizophoraceae)

[20, Simojovel and vicinity, Chiapas, Oligo–Miocene]

Gymnosperms: *Pinus* (few poorly preserved grains, Pinaceae), *Podocarpus* (Podocarpaceae). Angiosperms (dicotyledons): *Engelhardia* [*Alfaroa–Oreomunnea*, Juglandaceae], *Pachira* (Bombacaceae), *Pelliceria* (Pelliceriaceae), *Rhizophora* (Rhizophoraceae)

[21, Simojovel, Chiapas; Oligo–Miocene, La Quinta Formation]

Ferns and allied groups: *Ceratopteris* (Pteridaceae), monolete fern spores (*Verrucatosporites*), *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae), *Sphaeropteris–Trichipteris*[1] (Cyatheaceae), Vittariaceae (cf. *Antrophyum*). Gymnosperms: *Picea* (Pinaceae; few, corroded). Angiosperms (monocotyledons): cf. *Cryosophila* (Palmae), Palmae. Angiosperms (dicotyledons): *Alfaroa–Oreomunnea* (Juglandaceae), Bombacaceae (cf. *Aguiaria* type), *Cedrela* (Meliaceae), *Crudia* (Leguminosae), Ericaceae, *Eugenia–Myrcia* (Myrtaceae), *Guarea* (Meliaceae), *Pelliceria* (Pelliceriaceae), *Rhizophora* (Rhizophoraceae)

[22, DSDP Leg 66, Site 493 (offshore from Acapulco), early Miocene through Holocene]

Zone 1 (Holocene)—Ferns and allied groups: Fern spores (undifferentiated). Gymnosperms: *Pinus* (Pinaceae). Angiosperms (dicotyledons): *Quercus*
Zone 2 (Quaternary)—Ferns and allied groups: *Triletes*. Angiosperms (monocotyledons): Cyperaceae, Gramineae. Angiosperms (dicotyledons): *Hedyosmum* (Chloranthaceae). Incertae sedis: *Concentricystis*, *Foraminisporis* cf. *F. foraminis*, *Triplanosporites*
Zone 3 (late Pliocene)—Angiosperms (dicotyledons): *Ambrosia* type

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. *(Continued)*

(Compositae), *Artemisia* type (Compositae), *Helianthus* type (Compositae), Sapotaceae
Zone 4 (early Pliocene)—Ferns and allied groups: Fern spores (undifferentiated), *Polypodiisporites*. Angiosperms (dicotyledons): *Multiaerolites formosus* [Acanthaceae, *Justicia* type], *Quercus* (?; Fagaceae)
Zone 5 (late Miocene)—Angiosperms (dicotyledons): *Pachydermites diederixi* [Guttiferae, *Symphonia*]
Zone 6 (early Miocene)—Ferns and allied groups: *Echinatisporites* cf. *E. bockwitzensis* [*Selaginella*, Selaginellaceae], *Lepidosorus*, *Polypodiisporites favus*, *P. undulatus*, *Undulatisporites undulapolis*. Angiosperms (monocotyledon): *Proxapertites* (Palmae). Angiosperms (dicotyledons): *Bombax* (Bombacaceae), *Jussitriporites* cf. *undulatus* (Onagraceae), *Pachydermites diederexi* [*Symphonia*, Guttiferae]
Zone 7 (early Miocene)—Ferns and allied groups: *Echinatisporites* [*Selaginella*, Selaginellaceae], *Lepidosorus*. Angiosperms (dicotyledons): *Helianthus* type (Compositae)
Zone 8 (early Miocene)—Ferns and allied groups: *Echinatisporites* [*Selaginella*, Selaginellaceae], *Lepidosorus*, *Polypodiisporites*. Angiosperms (dicotyledons): *Helianthus* type

[23, Ixtapa, Chiapas, middle to late Miocene, Ixtapa Formation, under Oligo–Miocene, Miocene in Appendices 2.1, 2.2]

Ferns and allied groups: *Anemia* (Schizeaceae), *Cyathea* (Cyatheaceae), *Hemitelia* [*Cnemidaria*] (Cyatheaceae), *Lycopodium* (Lycopodiaceae), *Polypodium* [Blechnaceae–Polypodiaceae–Pteridaceae], *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae). Gymnosperms: Cycadaceae, *Pinus* (Pinaceae). Angiosperms (monocotyledons): Gramineae (*Monoporites*), *Liliacidites* (Bromeliaceae/Liliaceae), *Tillandsia* (Bromeliaceae). Angiosperms (dicotyledons): *Ayenia* (Sterculiaceae), *Carya* (Juglandaceae), *Engelhardia* [*Momipites*, *Alfaroa–Oreomunnea*; Juglandaceae], *Eperua* (Leguminosae), *Ilex* (*Ilexpollenites*; Aquifoliaceae), *Norantea* (Marcgraviaceae), *Pelliceria* (*Psilatricolporites*, Pelliceriaceae), *Rhizophora* (*Zonocostites*, Rhizophoraceae)

Megafossils

[24, Palomares, Oaxaca, and San José del Carmen, Veracruz, middle Miocene, formation not cited; under Oligo–Miocene, Miocene in Appendices 2.1, 2.2]

Fern and allied groups: *Acrostichum mexicanum* (Pteridaceae), *Gymnogramme(a)* [*Hemionitis*] *wadii* (Pteridaceae; now distributed among other genera). Angiosperms (monocotyledons): palm rays (Palmae). Angiosperms (dicotyledons): *Allamanda carmensis* (Apocynaceae), *Anacardites lanceolatus* (Anacardiaceae), *An(n)ona saraviana* (Annonaceae), *Apocynophyllum mexicanum* (Apocynaceae), *Bignonoides orbicularis* (Bignoniaceae), *Cedrela miocenica* (Meliaceae), *Connarus carmenensis* (Connaraceae), *Coussapoa veracruziana* (Urticaceae), *Crescentia cucurbitinoides* (Bignoniaceae), *Dioclea*(?) *mexicana* (Leguminosae), *Drypetes elliptica* (Euphorbiaceae), *Fagara wadii* (Rutaceae), *Ficus talamancana* (Moraceae), *Goeppertia* cf. *tertiaria* (Lauraceae [Marantaceae]), *Gouania miocenica* (Rhamnaceae), *Guettarda cookei* (Rubiaceae), *Inga miocenica* (Leguminosae), *Lecythidophyllum couratarioides* (Lecythidiaceae), *Leguminosites mexicanus*, *L. oaxacensis* (Leguminosae), *Liquidambar incerta* (Hamamelidaceae), *Melastomites angustus*, *M. obovatus* (Melastomataceae), *Mespilodaphne palomaresensis* (Lauraceae), *Moquilea mexicana* (Chrysobalanaceae), *Myrcia saraviana* (Myrtaceae), *Nectandra areolata*, *N. tehuantepecensis* (Lauraceae), *Rondeletia* (?; Rubiaceae), *Simaruba veracruziana* (Simaroubaceae)

[25, Mint Canyon, California, late Miocene; under Oligo–Miocene, Miocene in Appendices 2.1, 2.2; species names in parentheses are modern species considered related by Axelrod, 1979]

Dry tropical forest elements: Angiosperms (dicotyledons): *Cardiospermum* (Sapindaceae), *Cassia* (Leguminosae), *Laurocerasus* (Rosaceae), *Persea* (Lauraceae), *Robinia* (Leguminosae), *Sapindus* (Sapindaceae), *Thouinia* (Sapindaceae); Sclerophyll woodland, Angiosperms (monocotyledons): *Brahea* (Palmae), *Dichromena* (Cyperaceae), *Typha* (Typhaceae), Angiosperms (dicotyledons): *Acacia* (Leguminosae), *Acalypha* (Euphorbiaceae), *Aesculus* (Hippocastanaceae), *Arctostaphylos* (Ericaceae), *Baccharis* (Compositae), *Brickellia* (Compositae), *Bursera* (Burseraceae), *Caesalpinia* (Leguminosae), *Cardiospermum* (Sapindaceae), *Ceanothus* (Rhamnaceae), *Celtis* (Leguminosae), *Cercocarpus* (Rosaceae), *Chiococca* (Rubiaceae), *Colubrina* (Rhamnaceae), *Comarostaphylis* (Ericaceae), *Condalia* (Rhamnaceae), *Crossosoma* (Crossosomataceae), *Dalea* (Leguminosae), *Diospyros* (Ebenaceae), *Dodonaea* (Sapindaceae), *Euphorbia* (Euphorbiaceae), *Eysenhardtia* (Leguminosae), *Fendlera* (Hydrangeaceae), *Forestiera* (Oleaceae), *Fouquieria* (Fouquieriaceae), *Fraxinus* (Oleaceae), *Fremontodendron* (Sterculiaceae), *Holodiscus* (Rosaceae), *Ilex* (Aquifoliaceae), *Juglans* (Juglandaceae), *Laurocerasus* (Rosaceae), *Lippia* (Verbenaceae), *Lyonothamnus* (Rosaceae), *Lysiloma* (Leguminosae), *Mahonia* (Berberidaceae), *Pachycormus* (Anacardiaceae), *Passiflora* (Passifloraceae), *Persea* (Lauraceae), *Piscidia* (Leguminosae), *Pistacia* (Anacardiaceae), *Pithecellobium* (Leguminosae), *Platanus* (Platanaceae), *Populus* (Salicaceae), *Prunus* (Rosaceae), *Quercus* (Fagaceae), *Rhamnus* (Rhamnaceae), *Rhus* (Anacardiaceae), *Robinia* (Leguminosae), *Salix* (Salicaceae), *Sapindus* (Sapindaceae), *Schaefferia* (Celastraceae), *Tapirira* (Anacardiaceae), *Thouinia* (Sapindaceae), *Vitis* (Vitaceae); Semidesert, Angiosperms (monocotyledons): *Brahea* (Palmae), Angiosperms (dicotyledons): *Acacia* (*A. californica*, *A. pringleii*; Leguminosae), *Acalypha* (Euphorbiaceae), *Baccharis* (*B. sergiloides*, Compositae), *Bursera* (*B. laxiflora*, *B. odoratum*; Burseraceae), *Cardiospermum* (*C. halicacabum*, Sapindaceae), *Celtis* (*C. pallida*, *C. reticulata*; Ulmaceae), *Cercocarpus* (*C. paucidentatus*, Rosaceae), *Chiococca* (Rubiaceae), *Colubrina* (*C. glabra*, Rhamnaceae), *Condalia* (*C. lycioides*, *C. parryi*; Rhamnaceae), *Crossosoma* (*C. bigelovii*, Rosaceae [Crossosomataceae]), *Diospyros* (*D. palmeri*, Ebenaceae), *Dodonaea* (*D. angustifolia*, Sapindaceae), *Euphorbia* (*E. californica*, Euphorbiaceae), *Eysenhardtia* (*E. orthocarpa*, Leguminosae), *Fendlera* (*F. rupicola*, Hydrangeaceae), *Forestiera* (*F. reticulata*, Oleaceae), *Fouquieria* (*F. splendens*, Fouquieriaceae), *Lippia* (*L. palmerii*, Verbenaceae), *Lysiloma* (*L. candida*, Leguminosae), *Pachycormus* (*P. discolor*, Anacardiaceae), *Piscidia* (*P. mollis*, Leguminosae), *Pithecellobium* (Leguminosae), *Quercus* (*Q. turbinella*, *Q. brandegeii*; Fagaceae), *Rhamnus* (*R. pirifolia*, Rhamnaceae), *Rhus* (*R. microphylla*, Anacardiaceae), *Tapirira* (Anacardiaceae); Gallery forest, Angiosperms (dicotyledons): *Juglans* (*J. rupestris*, Juglandaceae), *Lyonothamnus* (*L. floribundus*, Rosaceae), *Platanus* (*P. racemosa*, Platanaceae), *Populus* (*P. arizonica*, Salicaceae), *Salix* (*S. exiga*, *S. lasiolepis*; Salicaceae)

Pliocene (5.3–2.6 Ma)

Microfossils

[26, Coatzacoalcos, Veracruz, Mexico, middle Pliocene, Paraje Solo Formation]

Ferns and allied groups: *Alsophila* (Cyatheaceae), *Ceratopteris* (Pteridaceae), *Cnemidaria* (*Hemitelia*, Cyatheaceae), *Cyathea* (Cyatheaceae), *Dicranopteris* (Gleicheniaceae), *Lomariopsis* (*Stenochlanea*, Dryopteridaceae), *Lycopodium* (Lycopodiaceae), other monolete fern spores (*Laevigatosporites*, *Verrucatosporites*), other trilete fern spores, *Pityrogramma* [possibly *Anemia*; Pteridaceae], *Psilotum* (Psilotaceae), *Selaginella* (Selaginellaceae), *Sphaeropteris–Trichipteris* (Cyatheaceae).[1] Gymnosperms: *Abies* (Pinaceae), *Picea* (Pinaceae), *Pinus* (Pinaceae), *Podocarpus* (Podocarpaceae). Angiosperms (monocotyledons): cf. *Astrocaryum* (Palmae), cf. *Attalea* (Palmae), cf. *Brahea* (Palmae), cf. *Chamaedorea* (Palmae), Cyperaceae, Gramineae, *Maximiliana* type (Palmae), *Smilax* (Smilacaceae), *Spathiphyllum* (Araceae). Angiosperms (dicotyledons): *Acacia* (Leguminosae), *Alchornea* (Euphorbiaceae), *Alnus* (Betulaceae), *Alfaroa–Oreomunnea* (Juglandaceae), cf. *Alibertia* (Rubiaceae), *Allophylus* (Sapindaceae), cf. *Bernardia* (Euphorbiaceae), *Borreria* (Rubiaceae), *Bravaisia* (Acanthaceae), cf. *Bredemeyera* (Polygalaceae), *Bursera* (Burseraceae), *Bue(y)ttneria* (Sterculiaceae), *Casearia* (Flacourtiaceae), *Cedrela* (Meliaceae), *Celtis* (Ulmaceae), chenoam, *Cleyera* (Theaceae), *Coccoloba* (Polygonaceae), *Combretum–Terminalia* (Combretaceae), *Comocladia* (Acanthaceae), Compositae, *Cupania* (Sapindaceae), *Cuphea* (Lythraceae), *Daphnopsis* (Thymelaeaceae), *Dichapetalum* (Dichapetalaceae), *Eugenia–Myrcia* (Myrtaceae), *Faramea* (Rubiaceae), *Guarea* (Meliaceae), *Gustavia* (Lecythidaceae), *Hampea–Hibiscus* [probably *Hibiscus tiliaceus*, Malvaceae], *Hedyosmum* (Chloranthaceae), *Hiraea* (Malpighiaceae), *Ilex* (Aquifoliaceae), *Iresine* (Amaranthaceae), *Juglans* (Juglandaceae), *Justicia* (Acanthaceae), *Laetia* (Flacourtiaceae), *Laguncularia* (Combretaceae), *Liquidambar* (Hamamelidaceae), *Ludwigia* (Onagraceae), *Malpighia* (Malpighiaceae), *Matayba* (Sapindaceae), cf. *Meliosma* (Sabiaceae), cf. *Mezia* (?) type (Malpighiaceae), *Mimosa* (Leguminosae), *Mortoniodendron* (Tiliaceae), *Myrica* (Myricaceae), *Passiflora* (Passifloraceae), cf. *Paullinia* (Sapindaceae), *Populus* (Salicaceae), cf. *Protium* (Burseraceae), *Quercus*

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. *(Continued)*

(Fagaceae), *Rajania* (Dioscoreaceae), *Rhizophora* (Rhizophoraceae), cf. *Sapium* (Euphorbiaceae), cf. *Securidaca* (Polygalaceae), cf. *Stillingia* (Euphorbiaceae), *Struthanthus* (Loranthaceae), *Symphonia* (Guttiferae), *Terebraria* (Rubiaceae), cf. *Tetrorchidium* (Euphorbiaceae), *Thalictrum* (Ranunculaceae), cf. *Tithymalus* (Euphorbiaceae), *Tournefortia* (Boraginaceae), *Ulmus* (Ulmaceae), *Utricularia* (Lentibulariaceae)

[Cenozoic undifferentiated, probably Tertiary]

Palmoxylon (4.1-41), *Acacioxylon* (4.1-41), *Juglans* (Juglandaceae; 4.1-42)

Quaternary (~2.6 Ma–Present)

Megafossils

[27, Cerro de La Estrella, Distrito Federal, Mexico, Pleistocene]

Angiosperms (dicotyledons): *Arbutus* (Ericaceae), *Buddlei(j)a cordata* (Loganiaceae), *Quercus hahnii*, *Q. hartwegii*, *Q. laeta*, *Q. laurina*, *Q. repanda*, *Q. rugosa*, *Q. rugulosa* (Fagaceae), *Ribes* (Grossulariaceae [Saxifragaceae]), *Salvia polystachia* (Labitatae), *Senecio* (Compositae), *Symphoricarpos microphyllus* (Caprifoliaceae)

[28, Packrat midden plant parts/fragments (for general discussion of packrat middens see I: pp. 135–136 and references therein; for explanation of bracketed letters see legend Table 4.1)]

Trees and large shrubs—Gymnosperms: *Juniperus californica* (Cupressaceae), *Pinus edulis–P. remota* (Pinaceae) [a]. Angiosperms (dicotyledons): *Acacia greggii* (Leguminosae), *Bursera microphylla* (Burseraceae), *Cercidium floribundum*, *C. floridum* [b], *C. microphyllum* (Leguminosae), *Horsfordia newberryi* (Malvaceae) [b], *Justicia californica* (Acanthaceae) [b], *Krameria grayi* (Krameriaceae) [b], *Olneya tesota* (Leguminosae), *Prosopis velutina* (Leguminosae), *Simmondsia chinensis* (Simmondsiaceae [Buxaceae]) [b], *Solanum hindsianum* (Solanaceae) [b], *Stegnosperma halimifolium* (Phytolaccaceae) [b]
Shrubs—Gymnosperm: *Ephedra nevadensis* (Ephedraceae). Angiosperms (dicotyledons): *Bebbia juncea* (Compositae), *Chrysothamnus teretifolius* (Compositae), *Encelia farinosa* (Compositae), *Eriogonum fasciculatum* (Polygonaceae), *Euphorbia misera* (Euphorbiaceae) [b], *Fouquieria columnaris* [b], *F. splendens* (Fouquieriaceae), *Hymenoclea salsola* (Compositae), *Hyptis emoryi* (Labiatae), *Jatropha* cf. *cuneata* (Euphorbiaceae), *Larrea divaricata* (Zygophyllaceae), *Lycium* (Solanaceae)
Subshrubs and parasites—Angiosperms (dicotyledons): *Ambrosia chenopodiifolia* [b], *A. deltoidea*, *A. dumosa* (Compositae), *Argythamnia* cf. *lanceolata* (Euphorbiaceae), *Brickellia atractyloides*, *B. coulteri* (Compositae), *Ditaxis lanceolata* (Euphorbiaceae) [b], *Eriogonum wrightii* (Polygonaceae), *Fagonia pachyacantha* (Zygophyllaceae) [b], *Galium stellatum* (Rubiaceae), *Galvezia juncea* (Scrophulariaceae) [b], *Hofmeisteria fasciculata* [b], *H. pluriseta* (Compositae), *Peucephyllum schottii* (Compositae), *Phoradendron californicum* (Loranthaceae), *Pleurocoronis laphamiodes* (Compositae) [b], *Porophyllum gracile* (Compositae) [b], *Trixis californica* (Compositae), *Viguiera* cf. *deltoidea*, *V. laciniata* (Compositae) [b]
Succulents—Angiosperms (monocotyledons): *Agave deserti*, *A. subsimplex* (Agavaceae) [b]
Cactaceae—*Carnegiea gigantea*, *Echinocereus*, *Ferocactus cylindraceus*, *Lophocereus schottii* [b], *Mammillaria grahamii* [b], *M. microcarpa*, *Opuntia arbuscula* [b], *O. bigelovii*, *O. fulgida*, *O. kunzei*, *O. ramosissima*, *Pachycereus pringlei* [b]
Gramineae—*Aristida adscensionis*, *Bouteloua aristidoides*, *B. barbata*, *Erioneuron pulchellum*, *Hilaria rigida*, *Muhlenbergia microsperma*, *Stipa speciosa*, *Vulpia*
Herbaceous perennials—*Euphorbia* cf. *polycarpa* (Euphorbiaceae), *Lyrocarpa coulteri* (Cruciferae), *Mirabilis bigelovii* (Nyctaginaceae), *Nicotiana trigonophylla* (Solanaceae), *Orobanche cooperi* (Orobanchaceae), *Verbena* (Verbenaceae)
Perennial–annual herbs—*Allionia incarnata* (Nyctaginaceae), *Argythamnia* cf. *neomexicana* (Euphorbiaceae), *Euphorbia pediculifera* (Euphorbiaceae), *Nicotiana* (Solanaceae), *Physalis* (Solanaceae), *Sphaeralcea* (Malvaceae)
Annuals—*Amsinckia tessellata* (Boraginaceae), *Amaranthus* (Amaranthaceae), *Argythamnia serrata* (Euphorbiaceae), *Astragalus nuttalianus* (Leguminosae), *Boerhavia wrightii* (Nyctaginaceae), *Camissonia clavaeiformis* (Onagraceae), *Chaenactis* cf. *stevioides* (Compositae), *Chorizanthe brevicornu*, *C. corrugata* (Polygonaceae), *Cryptantha barbigera*, *C. decipiens*, *C. maritima*, *C. pterocarya* (Boraginaceae), *Dalea mollis*, *D. mollissima* (Leguminosae), *Dicoria canescens* (Compositae), *Draba cuneifolia* (Cruciferae), *Eschscholzia* (Papaveraceae), *Gilia* (Polemoniaceae), *Kallstroemia* (Zygophyllaceae), *Lepidium lasiocarpum* (Cruciferae), *Lotus strigosus* (Leguminosae), *Lupinus arizonicus*, *L. concinnus* (Leguminosae), *Mentzelia involucrata* (Loasaceae), *Parietaria hespera* (Urticaceae), *Pectis papposa* (Compositae), *Perityle emoryi* (Compositae), *Phacelia* (Hydrophyllaceae), *Plantago insularis* (Plantaginaceae), *Rafinesquia neomexicana* (Compositae)

Microfossils

Northern Mexico

[29, San Felipe Basin, Baja California]

Algae: *Spirogyra*, *Zygnema*. Ferns and allied groups: Fern spores (undifferentiated). Gymnosperms: *Abies* (Pinaceae), *Ephedra nevadensis* type, *E. trifuca* type (Ephedraceae), *Juniperus* (Cupressaceae), *Pinus* (Pinaceae). Angiosperms: aquatics–Cyperaceae, *Hydrocotyle* (Umbelliferae), *Polygonum* (Polygonaceae), *Potamogeton* (Potamogetonaceae), Ranunculaceae, *Typha* (Typhaceae), *Acalypha* (Euphorbiaceae), *Agave* (Agavaceae), *Allionia incarnata* (Nyctaginaceae), *Ambrosia* (Compositae), *Arctostaphylos* (Ericaceae), *Artemisia* (Compositae), Asteraceae [Compositae] low spine, Asteraceae [Compositae] high spine, Cruciferae–Brassicaceae, *Bursera* (Burseraceae), Caryophyllaceae, chenoam, *Cirsium* (Compositae), *Eryngium* (Umbelliferae), *Galium* (Rubiaceae), Liguliflorae (Compositae), Onagraceae, *Plantago* (Plantaginaceae), Poaceae (Gramineae), Polemoniaceae, Portulacaceae, *Quercus* (Fagaceae), *Rhus* (Anacardiaceae), Rosaceae, Rubiaceae, *Sarcobatus* (Chenopodiaceae), *Thalictrum* (Ranunculaceae), Urticaceae

[30, Cuatro Ciénegas Basin, Coahuila]

Gymnosperms: *Abies*, Cupressaceae, *Ephedra*, *Picea*, *Pinus*. Angiosperms (monocotyledons): *Agave* (Agavaceae), Cyperaceae, Gramineae, Liliaceae, *Typha* (Typhaceae). Angiosperms (dicotyledons): *Artemisia*, other Compositae undifferentiated, Caprifoliaceae, *Celtis* (Ulmaceae–Moraceae), chenoams, *Eriogonum* (Polygonaceae), Euphorbiaceae, Onagraceae, *Polygala* (Polygalaceae), *Polygonum* (Polygonaceae), *Prosopis* (Leguminosae), *Quercus* (Fagaceae), Rosaceae, *Sarcobatus* (Chenopodiaceae), Solanaceae, *Tidestromia* (Amaranthaceae), Umbelliferae

Central Mexico

[Basins of the Transvolcanic Belt and vicinity (31–37), Tehuantepec (38), Yucatán (39, 40). * = Fossil spores of many genera of Blechnaceae–Polypodiaceae–Pteridaceae and pollen of the Cupressaceae–Taxaceae–Taxodiaceae, Chenopodiaceae–Amaranthaceae, *Carpinus–Corylus–Ostrya*, *Combretum–Terminalia* (Combretaceae; Graham, 1980), and *Eugenia–Myrcia* and other Myrtaceae (Graham, 1980) are difficult to impossible to distinguish. Tentative identifications can be suggested if the fossil deposits are sufficiently recent that the specimens likely represent extant local vegetation.]

References

Taxon	31	32	33	34	35	36	37	38	39/40
Algae									
Botryococcus		x							
Pediastrum		x	x						

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. *(Continued)*

	References								
Taxon	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39/40**
Spirogyra		x							
Zygnema		x							
Ferns and allied groups									
Isoetes (Isoetaceae)		x				x			
Selaginella (Selaginellaceae)		x		x					
**Asplenium* (Aspleniaceae)		x							
Dryopteris (Dryopteridaceae)									x
Hymenophyllum (Hymenophyllaceae)								x	
**Polypodium* (Polypodiaceae)		x							
**Pteridium* (Dennstaedtiaceae)						x			
Gymnosperms									
Abies (Pinaceae)	x	x	x	x		x		x	
Cupressus–Juniperus (Cupressaceae)		x	x	x		x	x		x
Picea (Pinaceae)	x	x	x						
Pinus (Pinaceae)	x	x	x	x	x	x	x	x	x
Podocarpus (Podocarpaceae)		x							
Taxodium (Taxodiaceae)	x								
Tsuga (Pinaceae)		x							
Angiosperms									
Acalypha (Euphorbiaceae)									x
Alfaroa–Oreomunnea (Juglandaceae)		x						x	x
Alnus (Betulaceae)	x	x	x	x	x	x	x	x	x
Ambrosia (Compositae)		x				x	x		x
Anacardiaceae			x	x					x
Arceuthobium (Loranthaceae)		x	x	x		x			
cf. *Argemone* (Papaveraceae)			x						
Artemisia (Compositae)		x		x		x			
Bignoniaceae							x		
Bombacaceae				x					
Boraginaceae			x						
Bravaisia (Acanthaceae)									x
Brosimum (Moraceae)									x
Bursera (Burseraceae)		x	x				x		x
Byrsonima (Malpighiaceae)									x
Cactaceae									x
Caprifoliaceae							x		
Carpinus–Corylus–Ostrya (Betulaceae)	x	x	x	x		x			
Carya (Juglandaceae)		x	x				x		
Caryophyllaceae			x				x		x
Cecropia (Urticaceae)									x
Celtis (Ulmaceae)			x				x		x
Ceratophyllum (Ceratophyllaceae)						x			
Chaetoptelea (Ulmaceae)									x
Chenoam	x	x	x	x	x	x	x	x	x
Chlorophora (Moraceae)									x
Compositae	x	x	x	x	x	x	x	x	x
Convolvulaceae							x		
Cordia (Boraginaceae)									x
Cruciferae			x						
Cuphea (Lythraceae)			x						
Cyperaceae	x	x	x		x	x		x	x
Dalbergia (Leguminosae)									x
Dodonaea (Sapindaceae)			x	x					
Eichornia (Pontederiaceae)									x

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. *(Continued)*

	References								
Taxon	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39/40**
Engelhardia [= *Alfaroa–Oreomunnea*] (Juglandaceae)	x							x	x
Ericaceae			x	x					
Eryngium (Umbelliferae)				x			x		
Euphorbiaceae			x	x			x		
Fagus (Fagaceae)		x	x						
Fraxinus (Oleaceae)		x	x	x		x			
Garryaceae			x						
Geraniaceae			x						
Gramineae	x	x	x	x	x	x	x	x	x
Gymnopodium (Polygonaceae)									x
Hedyosmum (Chloranthaceae)								x	
cf. *Hydrocotyle* (Umbelliferae)			x						
Ilex (Aquifoliaceae)	x	x							
Ipomoea (Convolvulaceae)							x		
Juglans (Juglandaceae)	x	x		x		x		x	
Labiateae		x					x		
Leguminosae							x		
Lemna (Lemnaceae)		x							
Liquidambar (Hamamelidaceae)		x	x					x	x
Malvaceae			x				x		x
Maydeae			x						
Melastomataceae									x
Mimosa (Leguminosae)									x
Mimosoideae							x		
Moraceae									x
Myrica (Myricaceae)			x	x					x
Myriophyllum (Haloragaceae)			x						
cf. *Nymphoides* (Menyanthaceae)			x						
Onagraceae			x				x		
Palmae									x
Papaveraceae							x		
Papilionaceae			x				x		
Phyllostylon (Ulmaceae)									x
Phytolaccaceae			x						
Piscidia (Leguminosae)									x
Plantago (Plantaginaceae)			x	x					
Polygonaceae		x					x		
Polygonum (Polygonaceae)			x						
Potamogeton (Potamogetonaceae)		x	x			x			x
Proteaceae									x
Quercus (Fagaceae)	x	x	x	x	x	x	x	x	x
Ranunculaceae			x						
Rhizophora (Rhizophoraceae)								x	x
Ribes (Grossulariaceae)							x		
Rosaceae			x						
Rubiaceae							x		
Ruppia maritima (Ruppiaceae)		x							
Sagittaria (Alismataceae)		x							
Salix (Salicaceae)	x	x		x		x	x		
Sapotaceae									x

Table 4.1. Plant fossils from the Late Cretaceous and Cenozoic of Mexico. *(Continued)*

	References								
Taxon	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39/40**
Satureja (Labiatae)							x		
Scrophulariaceae							x		
Solanaceae			x						
Thalictrum (Ranunculaceae)		x	x	x		x			
Tilia (Tiliaceae)						x			
Trema (Ulmaceae)									x
Trophis (Moraceae)									x
Typha (Typhaceae)	x	x			x	x			x
Ulmus (Ulmaceae)		x	x						x
Umbelliferae		x	x				x		
Urticaceae			x	x					
Urticales									x
Utricularia (Lentibulariaceae)			x						
Valeriana (Valerianaceae)			x						
Zea (Gramineae)	x		x	x		x	x		x

[Note: Taxons for references 41 and 42 are listed under "Cenozoic undifferentiated, probably Tertiary"; see page 253.]

(Cross & Martínez-Hernández, 1980). The authors note that the specimens may not be indigenous to the rocks because the strata are deeply weathered and porous. This record would be noteworthy because the family is the most advanced of the angiosperms (Bremer, 1994; Hind & Beentje, 1996; Caligari & Hind, 1996), its confirmed fossil record otherwise begins in the Oligocene (but see Chapter 8), and it is not common or widespread until the early Miocene (Graham, 1996).

By the Eocene, the Gulf of Mexico coastline had receded eastward to the vicinity of Laredo–Nuevo Laredo and southward along the eastern slopes of the Sierra Madre Oriental and the Front Ranges and High Plateaus region of Chiapas (Fig. 1.10). In northeastern Mexico, the undulating Cretaceous subsurface topography created numerous shallow to moderately deep overlying Eocene cuencas (basins) of different sizes, variously interconnected to coastal habitats. Middle Eocene sediments from the Laredo Formation (Claiborne Group) in the Laredo Basin of south Texas contain a tropical to subtropical assemblage of shark, skates, rays, *Tarpon*, and Crocodylidae. The composition of the palynoflora is listed in Table 4.1. Of particular interest is pollen of the Old World tropical mangrove palm *Nypa*, presently found in India, southeastern Asia, the Philippines, and northern Australia (Queensland). It is known in the stratigraphic literature as *Spinozonocolpites prominatus* and has been reported from the Eocene of southwestern Europe, northwestern Africa, and several localities along the Gulf Coast (Westgate & Gee, 1990).

Immediately across the border in the vicinity of Nuevo Laredo, Tamaulipas, and at the nearby abandoned settlement of Colombia, Nuevo León, the basin is known as the Cuenca de Burgos. A map of northeastern Mexico (Fig. 1.5) shows Tamaulipas with a long westward projection extending along the Río Bravo (Río Grande), and Nuevo León with a narrow northward extension to the river where the town of Colombia was to be located. These geographic configurations were designed to give the northern states a border along the river and to make Nuevo León a port city, when it was deemed feasible to dredge the Río Bravo to a depth allowing ocean-going vessels to travel ~150 km upriver. Small amounts of coal and lignite were another inducement. Unfortunately, the river proved too shallow, the sediment load too heavy, dredging impractical and too costly, maintenance prohibitive, and the coal too scant to support the industrial complex envisioned. However, the Comisión Federal de Electricidad (C.F.E.) drilled several boreholes, and the palynomorphs were studied to determine the age and stratigraphic relationships of the underlying strata (Martínez-Hernández et al., 1980). The biological affinities of some specimens are reported to family, but the Eocene age and the generalized nature of the specimens requires an artificial nomenclature system for the palynomorphs (Table 4.1). As a generalization, the point at which a sufficient number of palynomorphs resemble modern taxa to allow use of the modern analog or NLR method is about the middle Eocene. Among the taxa reported are Schizaeaceae, possibly Bombacaceae, *Ilex*, Onagraceae, and *Momipites* (Juglandaceae). Little can be said about the flora except that it is typical of tropical to warm-temperate Eocene assemblages.

To the south in the state of Chiapas, the Eocene coastline was along the eastern flanks of the Front Ranges and High Plateaus region, fully 90 km inland from its present position.

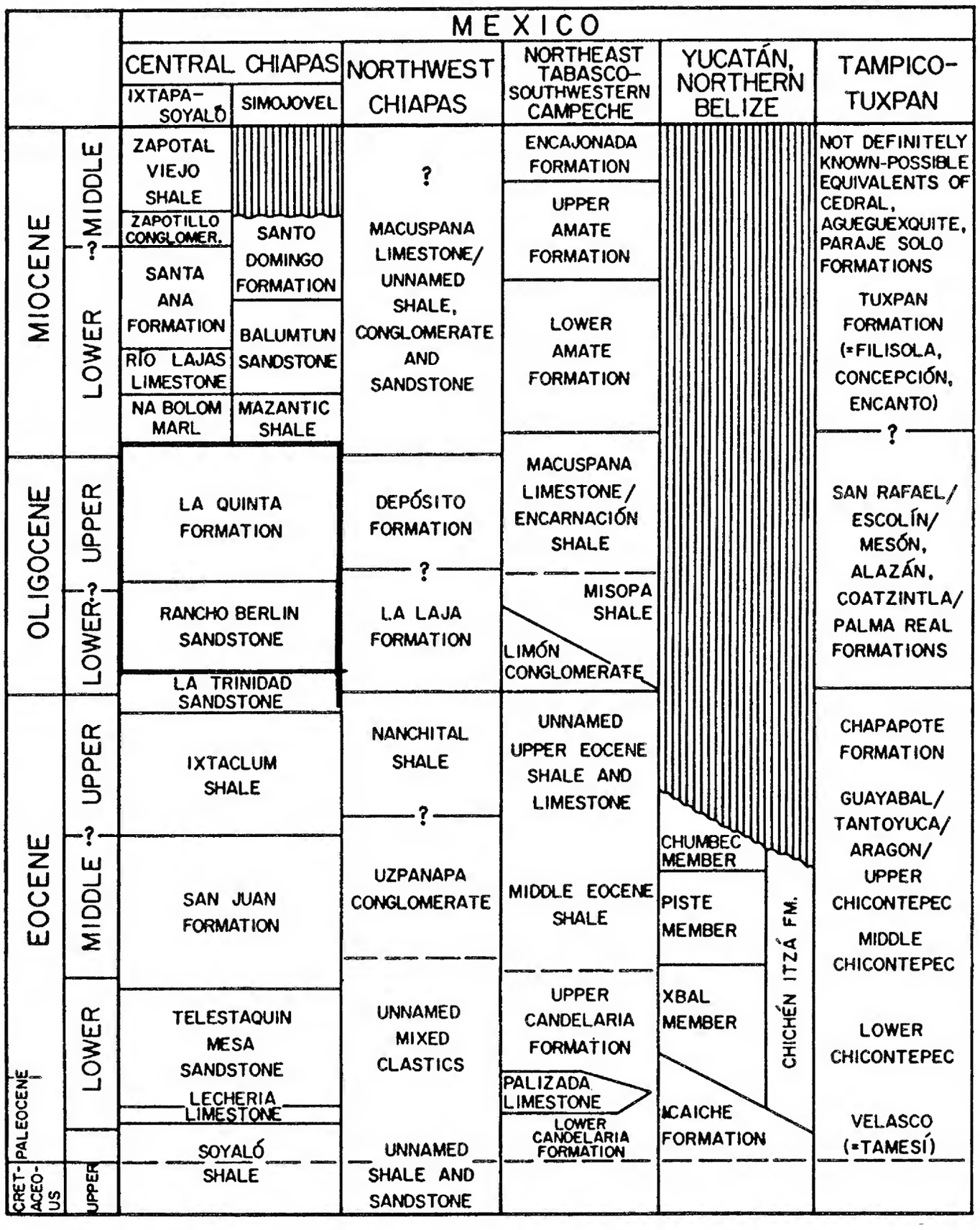


Figure 4.5. Stratigraphy and correlation of Tertiary strata in the region of Simojovel (after Frost & Langenheim, 1974, fig. 9). Used with permission of Northern Illinois University Press, DeKalb.

Sea levels were high due to the near absence of glaciers, but they fluctuated locally through regional tectonic activity. Rather than basins as in the north, the result in Chiapas was Eocene to Miocene sediments deposited along a retreating shoreline, with standstills that left seams of coastal lignites and fine-grained mineral sediments intermingled with near-shore marine deposits. These sediments are exposed along a zone running parallel to the Front Ranges from just north of Simojovel to Ixtapa (Fig. 1.10), and they contain shallow-water marine dinoflagellates and diverse palynomorph assemblages. The Eocene component of these floras is given in Table 4.1 along with the possible affinities of the plant microfossils. Among the taxa reported are *Momipites*, *Pelliceria*, and *Rhizophora*. Affinities are cited for other taxa unexpected in a tropical Eocene flora (e.g., *Abies*, *Cedrus*, *Podocarpus*). The lower Eocene El Bosque Formation is not listed in Frost and Langenheim (1974) as a formation (rather, it appears as a locality), and the palynomorphs are mostly cited as "escaso" ("scarce"; Tomasini-Ortiz & Martínez-Hernández, 1984). The upper Eocene La Trinidad Formation is at the Eocene–Oligocene boundary (Fig. 4.5).

Mangrove formation in Mexico in the Paleogene—Where rivers empty into oceans, and where tides inundate upriver habitats, brackish water environments are created and support mangrove vegetation. Plants tolerant of these conditions are found among the ferns (*Acrostichum*), palms (the Old World *Nypa*), and some 14 families of dicotyledons. In the Gulf of Mexico and Caribbean region today, the principal mangroves are *Avicennia*, *Conocarpus*, *Laguncularia*, and *Rhizopora*. *Pelliceria* occurs farther south in Central America and northern South America. In the Eocene, however, the composition of the mangrove formation was different. Coastal sediments of Paleocene through early Eocene age often contain high percentages of *Brevitricolpites variabilis* of unknown biological affinities, instead of *Rhizophora*, which first appears in the middle Eocene (Graham, 1995, 2006). Another difference is that *Nypa* grew in the north until the middle Eocene (the Lar-

edo–Burgos Basin floras), and *Pelliceria* in the south through the Oligocene and possibly into the middle Miocene (Chiapas floras). With the disappearance of *Nypa* and *Pelliceria* and the appearance of *Rhizophora* in the middle Eocene, the modern mangrove formation of Mexico was essentially established.

The Eocene assemblages from Mexico represent a vegetation distributed over a landscape of subdued topography, growing under warm-temperate to tropical climates without pronounced seasonality, and not sharply delineated into climatically or altitudinally defined communities. The principal differences were habitat-based and included brackish-water mangrove, freshwater, and terrestrial environments. A cool temperate association was already established in the southeastern United States in the Paleocene and Eocene, likely in the Appalachian uplands, and included *Abies*, *Pinus*, *Alnus*, *Betula*, *Carya*, *Castanea*, *Celtis*, *Fagus*, *Ilex*, *Juglans*, *Liquidambar*, *Liriodendron*, *Myrica*, *Nyssa*, *Ostrya–Carpinus*, *Platanus*, *Quercus*, *Tilia*, and *Ulmus*. None of these have been confirmed in the Paleogene of Mexico, or elsewhere in northern Latin America, with the possible exception of a poorly preserved grain of *Pinus* in the Laredo Formation of south Texas and the widespread *Ilex* (as *Ilexpollenites*) in the Burgos Basin flora of Nuevo León. If several diverse and well-preserved microfossil and megafossil floras were available from the Paleocene and the early to middle Eocene LPTM period, and from the late Eocene after the drop in global paleotemperatures (Fig. 4.3); and if these were studied by modern methodologies such as NLR, LMA (Royer & Wilf, 2006), and CLAMP; and if the climatic, biogeographic, and phylogenetic implications were conservatively interpreted within the context of established global conditions and events, then the development of vegetation between the Paleocene and the late Eocene could be better outlined. However, these floras are difficult to study, and they are transitional between ancient and more modern plant formations and between hothouse and icehouse climates, so the likelihood of this being achieved in the near future is remote. The database noticeably improves, however, in the Oligocene.

Figure 4.6. *Cercocarpus mixteca* (Rosaceae) from the Oligocene Pie de Vaca Formation, Tepexi de Rodríguez, Puebla, Mexico. Reprinted from Velasco de Léon and Cevallos-Ferriz (2000), used with permission of Elsevier Science Publishers, Amsterdam.

OLIGOCENE, OLIGO–MIOCENE, EARLY AND MIDDLE MIOCENE (33.7–11.2 MA)

Most plant fossils of Oligocene age can be assigned to modern families, many to modern genera, and some are morphologically similar to extant species. A threshold in the downward-trending global paleotemperature curve was reached in the early Oligocene (~33.7 Ma; e.g., continental glaciation in Greenland, 38–30 Ma, Eldrett et al., 2007), and MATs then fluctuated near the glacial–non-glacial boundary until the beginning of the middle Miocene (~16.4 Ma; I: p. 89; Fig. 4.3). Eccentricity cycles of 405,000, 127,000, and 96,000 years are detected in equatorial Pacific sediments (ODP Site 1218) and are believed to have amplified the global carbon cycle and contributed to the fluctuating climatic patterns of the Oligocene (Pälike et al., 2006). Under conditions of moderate temperatures and precipitation, factors such as the proximity of maritime environments, large temperature-buffering lakes, and variations in local topography, slope, exposure, rain shadows, and edaphic factors played a significant role in determining the plant associations present in a particular region. The volcanic island arc of proto-Baja California was accreted to the northwestern mainland in the Oligocene; there were hills and basins of moderate relief and depth in the Mesa Central; the Sierra Madre Occidental was in the upper volcanic phase of its development; in the Sierra Madre Oriental there was emplacement of volcanic rocks, peneplanation, volcanism, and block faulting; and overall the sierras were about half of their present elevation. The Transvolcanic Belt would not begin its principal period of development until the middle to late Miocene (~15 Ma).

Under these transitional conditions of climate and physiography, a megafossil flora was being deposited at Los Ahuehuetes, near Tepexi de Rodríguez, Puebla (Pie de Vaca Formation; 18°35'N, 97°55'W; Table 4.1; Pälike et al., 2006). The flora was initially thought to be Miocene to possibly lowermost Pleistocene in age (see Magallón-Puebla & Cevallos-Ferriz, 1993, p. 1163) based on erroneous mammal footprint evidence, while later palynological data were interpreted to suggest it could be as old as Eocene (Martínez-Hernández & Ramírez-Arriaga, 1999). The flora is now considered to be about late Oligocene in age. Both megafossils and microfossils are present, and because the number of different types of dicotyledon leaves exceeds ~30, it is statistically feasible to estimate the paleoclimate from foliar physiology as well as by the modern analog method (I: pp. 122–128). If cuticles are discovered, it may also be possible to make estimates of CO_2 concentration based on stomatal analysis (I: p. 128).

The flora provides paleobotanical information for a time (Oligocene) and place (eastern Transvolcanic Belt) where

data are scarce. Thus, it is tempting to see broad biogeographic, evolutionary, and paleoenvironmental implications as each new taxon is described. However, each megafossil is being meticulously studied, and only a few documented identifications are available. One member is *Eucommia*. The genus is presently native to western and central China, but in the Middle Tertiary it was widespread through Asia, Europe, and North America. When it was thought the Pie de Vaca flora could be Miocene in age and the last occurrence to the north was in the Beaverhead Basins and Metzel Ranch floras of Montana (considered lowermost Miocene), the occurrence in Puebla was the latest known for the New World. When the Pie de Vaca flora was later estimated to be Oligocene, that put its disappearance from both regions at about the same time. Now that the Montana floras are considered latest Eocene to earliest Oligocene (I: p. 210), the last known occurrence of *Eucommia* in the New World is again in Puebla, and that is presently the southernmost limit of the genus in the fossil record of the Americas.

Another specimen of taxonomic and biogeographic interest is *Haplorhus* (Anacardiaceae; Ramírez & Cevallos-Ferriz, 2002), presently treated as an endemic xerophyte of Peru. If it is a distinct genus, *Haplorhus* in the Pie de Vaca flora would either have been an intercontinental disjunct, or more widely distributed extending at least intermittently from Peru to Mexico. If it is eventually merged into another genus, a different pattern of distribution would emerge and a different set of explanations would be required to explain its history. The consequence of taxonomy for biogeography is discussed in I: pp. 327–328.

The fossils from the Los Ahuehuetes locality include a number of plants that today grow in seasonally dry and/or disturbed habitats (*Karwinskia*, Rhamnaceae; *Cercocarpus*, Rosaceae, Fig. 4.6; *Pseudosmodingium*, Ramírez et al., 2000; possibly *Haplorhus*), and others of similar ecology are presently under study (*Prosopis*, *Sophora*; Fabaceae). Reference is made to the presence of the extreme xerophyte *Larrea* (creosote bush) in pre-Pleistocene beds in California (unpublished data of V. Page from J. Wolfe; Ramírez & Cevallos-Ferriz, 2002). Localized xeric elements are known in western North America as early as the Eocene (e.g., in the middle Eocene Green River flora of Colorado–Utah; I: pp. 200–204), but they began coalescing into communities only in about the middle Miocene with waning CO_2 concentration, cooling temperatures, increasing continental glaciation in Antarctica, early glaciation in the Arctic, increasing seasonality, and associated dryness (I: ch. 6, 7). These conditions were augmented locally by topographic effects from orogeny, such as rain shadows, slope, exposure, and edaphic factors. Deserts of present-day aspect developed primarily in the Pliocene and were modernized during the dry intervals of the Quaternary. The reference to *Ephedra* and identifications from the Pie de Vaca flora of *Haplorhus*, *Prosopis*, and *Sophora* might suggest that the flora could represent a desert or near-desert assemblage, arid conditions had developed earlier and were more widespread than context information indicates, and the origin of floristic relationships between arid northern Mexico and the Monte region of Argentina was through dry habitat near-continuity rather than primarily by long-distance dispersal (Chapter 8, A Subhumid Corridor). How the Oligocene vegetation of Puebla, including mesic elements such as *Eucommia*, will eventually fit into the origin of interhemispheric patterns of dry vegetation is still under study. It is possible that the Pie de Vaca flora had local associations or phases, similar to those of the present *Nolina–Hechtia–Agave* desert on the border of Puebla and Veracruz, within a more mesic Oligocene setting. The paleovegetation would then be viewed as a mosaic growing under climatically and topographically moderate transitional conditions typical of the Oligocene. If further study reveals the Pie de Vaca flora was more arid, it would be interesting to consider if it is younger in age (e.g., Miocene) when such vegetation was becoming better defined and more widespread. Megafossils mentioned but not yet published for the flora are *Berhamniphyllum*, *Reinweberia* (Fabaceae), and *Statzia* (all extinct genera), and *Lysiloma* (bosque tropical caducifolio; shrubland/chaparral–woodland–savanna), *Populus*, and *Salix* (gallery forests; mesic).

Plant microfossils typically provide a more geographically inclusive picture of ancient communities because pollen and spores are brought, blown, or washed in from a variety of habitats. However, interpretation of basin assemblages, like the Pie de Vaca, is difficult, and plant microfossils alone usually allow a broad range in estimates of paleoenvironments and age. The usefulness of palynomorphs increases with precise, independent age estimates for the sediments; the likelihood of few or no reworked specimens; or recognition of such specimens by a combination of generally darker color, poorer preservation, fragmented condition, specimens that are typical of stratigraphically older or younger strata, associations that are ecologically suspect for the prevailing paleoclimates, and components that require a range in local physiogeography not supported by the geologic evidence. When the beds were considered possibly Eocene in age, the presence of *Abies* (fir), *Picea* (spruce), and *Betula* (birch) would be unexpected based on ecology, climate trends, and the uplift history of the Transvolcanic Belt. If the megafossils are interpreted to indicate a dry environment, (1) the pollen identified as mesic and marsh–wetland plants would be noteworthy, (2) pollen of northern hardwoods like *Carya*, *Castanea*, *Corylus*, *Juglans*, *Liquidambar*, and *Platanus* would be unexpected chronologically and ecologically (Chapter 8), and (3) pollen of the chenoams and Asteraceae (Chapter 8) would be of interest because they become most diverse and widespread in the Neogene. Finally, if the beds were Neogene and dry, pollen attributed to plants presently distributed in Indomalaya, Chile, and from the Himalayas to Formosa, and the Old World tropical *Pandanus*, would be unexpected. The plant microfossil composition of the flora as presently listed is given in Table 4.1.

Megafossils are described from two localities considered middle Miocene in age from the eastern Isthmus of Tehuantepec–San José del Carmen in Veracruz (~17°50'N, 94°45'W) and Palomares in Oaxaca (17°08'N, 95°03'W). Thirty-three

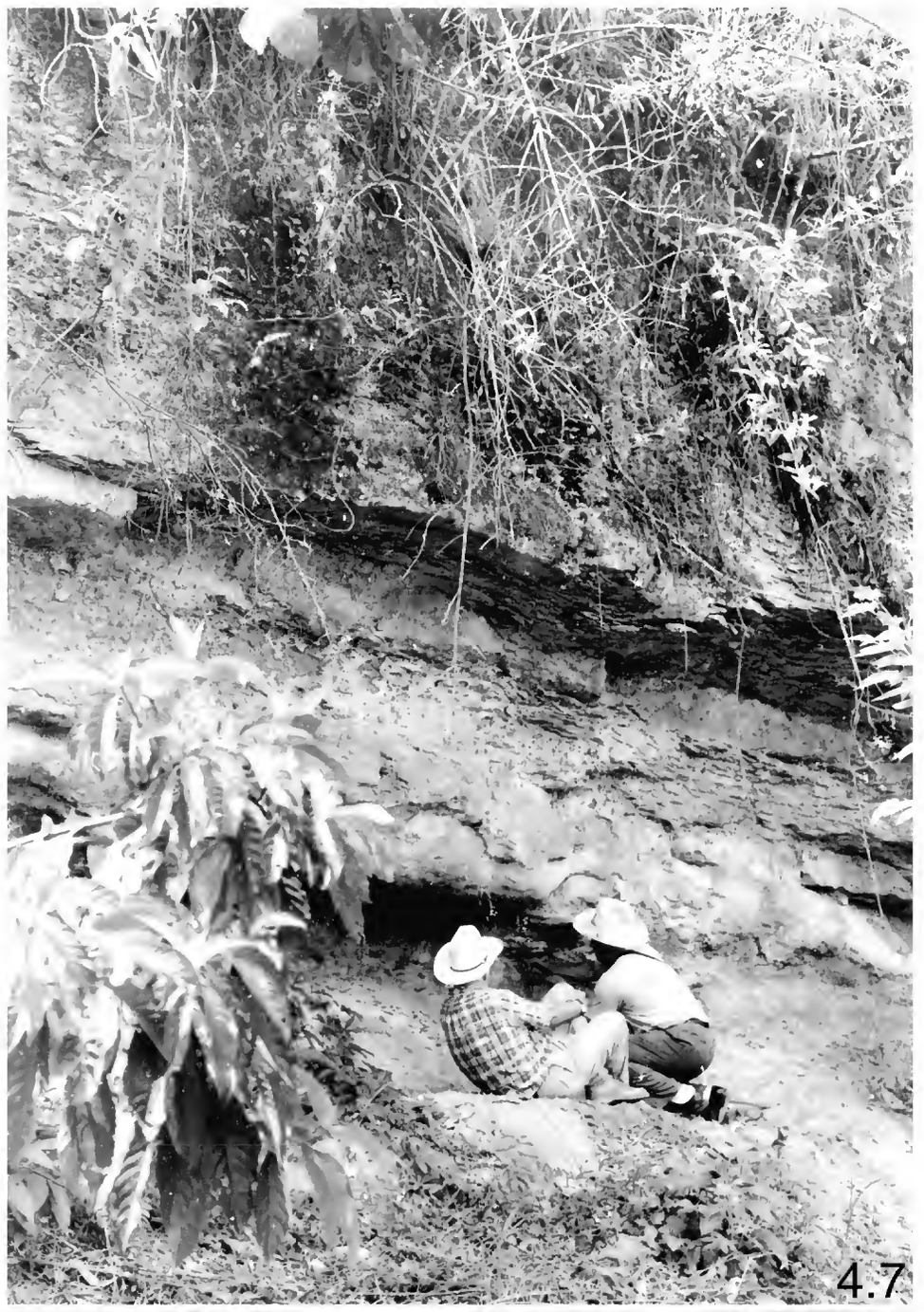
species are identified from sites where "detailed collecting would probably yield from 100 to 150 species" (Berry, 1923, p. 1). The illustrations show that virtually all species have entire margins, and even the number presently described is sufficient for LMA and CLAMP study. There is an associated marine fauna, the matrix of the specimens (at USNM) and sediments at the locality probably contain palynomorphs, and plant microfossils have already been described from slightly younger deposits to the north (Paraje Solo flora) and slightly older deposits to the south (Simojovel floras). If the age is correct, it places the flora near the beginning of a drop in global temperature, with the many climatic implications of that event, and near the time when significant altitudes in the eastern Transvolcanic Belt were developing. The assemblage seems ideal for revisionary studies using modern methods, but the specimens have not been examined for 80 years and it is not known if the locality still exists. The species recognized by Berry in 1923 are listed in Table 4.1.

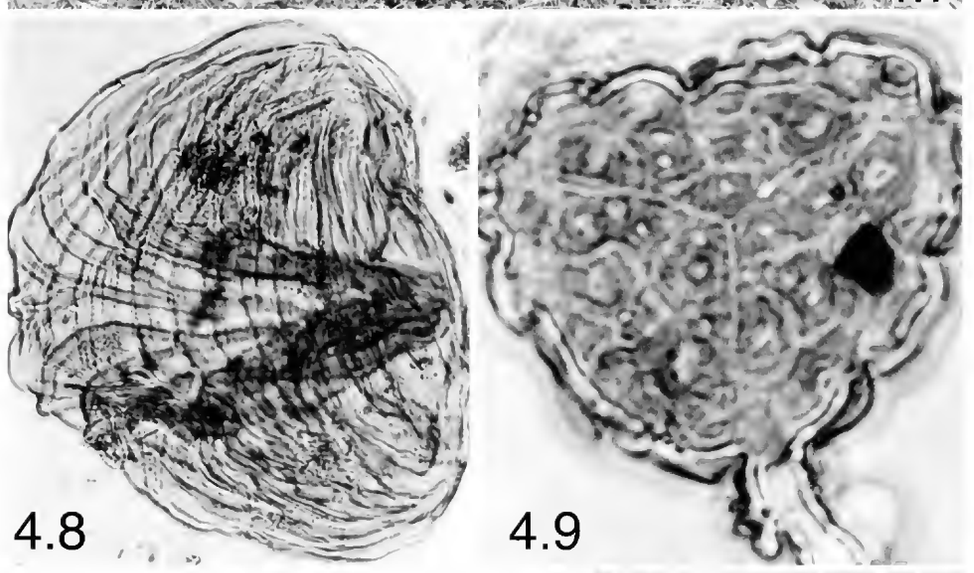
Farther to the south in Chiapas, Oligo–Miocene to Miocene floras are known from the border of Tabasco and Veracruz (93°30'N, 17°20'W; Pichucalco flora), and from just north of Simojovel to Ixtapa in the same vicinity as the Eocene material previously discussed. There are well-known amber deposits in the region, and a leaf of *Acacia* (Fabaceae), a fossil flower of *Tapirira* (Anacardiaceae), and two staminate flowers of *Socratea brownii* (Arecaceae) have been described (Miranda, 1963; Poinar, 2002). Infrared spectrophotometry has shown the amber to be from *Hymenaea* (Fabaceae; Langenheim, 1966), documenting the genus in the Oligo–Miocene of Chiapas. The Pichucalco microfossil flora is considered early to middle Miocene in age (Palacios Chávez & Rzedowski, 1993), and the composition is given in Table 4.1. It is said that 663 kinds of microfossils are identified (~6× or more than for any other Cenozoic assemblage in northern Latin America), and some of the identifications are suspect for a Neogene flora in southern Mexico, particularly *Davallia* (presently distributed in Europe, the Canary Islands, Madagascar, tropical Asia, tropical Pacific), *Sequoia* (California, Oregon), *Baikiaea* (tropical Africa), *Berula* (Europe, Central Asia, Iran), *Codiaeum* (Malaysia, Polynesia, northern Australia), *Kleinhovia* (tropical Asia), *Nothofagus* (New Guinea, New Caledonia, Australia, New Zealand, South America), *Nypa* (tropical Asia; *Spinozonocolpites*, the latest New World occurrence otherwise is in the Eocene), *Platycarya* (eastern Asia), and eight kinds of the stenopalynous Poaceae pollen. Other identifications are not so surprising, and a revision of this extensive flora would be worthwhile, based on an extensive reference collection of herbarium-vouchered material and interpreted within the context of geologic, climatic, and biogeographic trends and phylogenies (Chapter 7).

Plant microfossils were described by Langenheim et al. (1967) from the vicinity of Simojovel, later by Tomasini-Ortiz and Martínez-Hernández (1984) from several sites in the region, and most recently by Graham (1999a; Graham & Palacios Chávez, 1996) from sediments of the La Quinta Formation at Simojovel (Figs. 4.7–4.11; Table 4.1). Collectively, the Oligo–Miocene and early to middle Miocene fossils show vegetation just assembling into plant formations of modern aspect from the transition interval of the Oligocene as climates cooled, greater seasonality developed, and topography became more diverse. There is no evidence of extensive arid vegetation (desert, shrubland/chaparral–woodland–savanna; *Acacia* represents a possible dry element, but it ranges into other plant formations) and no evidence for extensive grassland. The coast was fringed by mangroves (*Pelliceria*, *Rhizophora*), and slightly inland there was aquatic vegetation (*Ceratopteris*, *Pachira*). Although elements of the lowland Neotropical rain forest were present (*Selaginella*, *Antrophyum*, *Pteris*, *Sphaeropteris–Trichipteris*,[1] *Crudia*, cf. *Guarea* type), the numerical abundance of these microfossils is low and the dominants were not found. The plants probably represent the low wet phase of a lower to upper montane broad-leaved forest that further included *Lycopodium*, *Podocarpus*, Poaceae (presently widespread in many communities), *Alfaroa–Oreomunnea* (= the form genus *Momipites*), *Cedrela*, Asteraceae, Ericaceae, possibly *Eugenia* (as *Eugenia–Myrcia*), *Hymenaea*, *Ilex*, Arecaceae, and *Tapirira*. Affinities cited for *Momipites* in the literature require some explanation. The small, oval-triangular, triporate, psilate grains are similar to modern *Alfaroa*, *Engelhardia*, and *Oreomunnea*. *Engelhardia* is now treated as an Old World genus, and the others are members of the montane forests of Mexico and Central America. It is not known from megafossils when *Engelhardia* disappeared from North America (probably by the Pliocene), or how far it may have extended into Latin America. *Momipites* in the Late Tertiary probably represents *Alfaroa* and *Oreomunnea*, while in older deposits it could also include *Engelhardia*.

The coniferous forest is represented by *Pinus*, but pollen of higher-altitude gymnosperms is rare and poorly preserved (*Picea*) or absent (*Abies*). There is no evidence of a deciduous forest association with northern temperate elements, or an elfin forest, ceja, or páramo, consistent with the geology and other paleofloras of the region.

The present average elevation at the La Quinta site at Simojovel in the Front Ranges and High Plateaus region of Chiapas is ~2000 m, and the highest peak is San Cristóbal de Las Casas at 3004 m. The earliest Miocene strata are folded and show evidence of compressive deformation, while Plio–Pleistocene rocks are horizontal and mostly undeformed. This brackets the principal time of uplift at between the early Miocene and the Plio–Pleistocene. The paleoelevation during La Quinta time is estimated at ~1000–1200 m. The flora was deposited at the continent-ocean interface in a region with less physiographic diversity than at present, closer in time to the more tropical conditions of the Paleogene, and prior to the inception of enhanced global cooling, drying, and seasonality at the end of the early Miocene. Present climatic conditions at Simojovel are a MAP of ~2500 mm (summer wet) and a relatively uniform MAT of 24° C at mid-elevations. Under the physical conditions noted earlier for La Quinta time, it is estimated that slightly higher temperatures (e.g., 25°–26° C) and precipitation (2700–3000 mm), less seasonality, maritime environments in





Figures 4.7–4.11. La Quinta Formation, Simojovel, Chiapas, Mexico. 4.7. Hillside exposure east of the Simojovel cemetery. Darker bands are seams of lignite from which most plant microfossils were recovered. Lighter bands are fine-grained sediments that at other nearby sites contain amber to which the local inhabitants have mining rights. Although permission had been obtained from workers in the nearby field, the collectors were held at gunpoint for about an hour until their non-commercial intentions had been clearly explained. 4.8. Spore of the floating aquatic fern *Ceratopteris*. 4.9. *Sphaeropteris–Trichipteris*. 4.10. *Crudia* (Leguminosae; *Striacolpites cataumbus* in the stratigraphic literature). 4.11. *Alfaroa–Oreomunnea* (*Momipites*).

the immediate vicinity of deposition, and a topography more subdued than at present would account for the principal plant formations.

C_4 pathways and grasslands in Mexico—In about the middle Miocene (15–14 Ma), a drop in global paleotemperatures marked the beginning of permanent continental ice on Antarctica and substantial glaciations in the Arctic (earliest are ~45 Ma; Moran et al., 2006). Aeolian dust begins to increase in ocean cores and in other sediments, and kaolinite records further reflect increasing dryness and seasonality associated with the cooling. Among the results were the expansion of grasslands in many parts of the world, a co-evolutionary response, and an increase in the number of ruminants. Many grasses use a photosynthetic pathway (C_4) influenced by a complex of factors such as atmospheric and oxygen concentration and temperature that differs from the pathway favored by many trees and shrubs. Each pathway produces a different carbon isotope signature in the plants, and this is preserved in the organic component of paleosols and in tooth enamel. Fox and Koch (2003) examined this signature in paleosols from the Great Plains, covering the past 23 Ma, and found that grasses were ~20% of the soil plant biomass through ~5 Ma, increasing to modern levels about 2.5 Ma (near the beginning of the Quaternary). Although there is no extensive fossil record of grasslands in Mexico, that record in the Great Plains of northern North America and context information provide a plausible basis for estimating the beginning of grasslands as a formation in Mexico at about the middle Miocene (~15 Ma) and later consolidation into a recognizable modern plant formation during the cold intervals of the Pliocene and especially in the Pleistocene. The oldest North American grasses are from the early Eocene of Tennessee (Crepet & Feldman, 1991; I: p. 170; see Prasad et al., 2005; Piperno & Sues, 2005 for discussion of grass phytoliths reported from Late Cretaceous coprolites of India).

Shrubland/chaparral–woodland–savanna and desert vegetation in Mexico—Most Asian exotic plants disappeared from North America in the late Miocene and Pliocene, probably due to reduced summer rainfall and greater seasonal dryness. The only late Miocene vegetation known for Mexico is, unexpectedly, preserved in the Mint Canyon flora (13 Ma) of southern coastal California. It is on the Pacific side of the San Andreas Fault system and has been transported northward from the Sonoran region of northwestern Mexico (Axelrod,

1940, 1979). Thus, it gives an indication of the vegetation and environment of the present Sonoran Desert near the time of increasing dryness and seasonality. The vegetation was an oak woodland with sclerophyllous shrubs and thorn forest elements (chaparral; Table 4.1). The MAP is estimated at 500 mm, somewhat lower (380–500 mm) in the central part of the Sonoran region, and perhaps drier in canyons to the lee of hills on Baja California, and warmer on south-facing slopes. The time of principal development of the shrubland/chaparral–woodland–savanna formation in Mexico began in about the middle Miocene (~15 Ma; Graham & Dilcher, 1995). Taxa preadapted to arid conditions are present in floras as old as the middle Eocene (Green River flora of Colorado–Utah), and they are numerous in the late Miocene Mint Canyon flora. As arid conditions expanded after the middle Miocene, these older elements constituted a reservoir from which the tropical dry forest and desert vegetation were assembled (e.g., *Tiquilia*; Moore & Jansen, 2006): "Thus, the area of the present Sonoran Desert has been accumulating taxa which were preadapted both in form and function to progressively increasing drought during the Tertiary" (Axelrod, 1979, p. vi). As mentioned, the modern version of the North American dry vegetation appeared primarily in the Mio–Pliocene and was modernized during the dry intervals of the Quaternary period. The same pattern is evident in the Taklimakan Desert of China, the second-largest desert in the world (337,000 km^2) after the Sahara, with shifting sand dunes evident at 5.3 Ma (viz., the beginning of the Pliocene; Sun & Liu, 2006).

Tracing the origin of the Mexican dry forest provides opportunity to emphasize the logic, as well as the necessity, of a systems approach to such complex problems. Two factors noted above are (1) the availability of types preadapted to seasonally dry environments, and (2) the spread of these environments beginning at about the end of the early Miocene. Other factors include lowering sea levels and rising landmasses that promote (3) continentality; orogeny that augments trends toward seasonally dry climates and promotes (4) rain shadows; and (5) increasing edaphic aridity through generation of coarse soils. Becerra (2005), using a time-calibrated phylogeny of *Bursera*, dates its diversification and radiation in northwestern Mexico at between 34 and 17 Ma, correlated with the development of the Sierra Madre Occidental, and at 13.5 Ma to the south, paralleling formation of the Transvolcanic Belt. *Bursera* is a prominent member of the Mexican dry forest (along with various legumes) and, therefore, Becerra (2005) places the beginnings of that forest at ~30 Ma. This is earlier than outlined above, and the assumed time of origin is attributed primarily to the appearance of high altitudes in the Mexican sierras.

Dick and Wright (2005) provide a cautionary note by asking, "Can the age of a single clade be used to infer the age of a biome?" They cite examples from *Inga*, Malpighiales, *Leucaena*, Sapindales, and *Commiphora* to illustrate different evolutionary rates within and among clades and biomes in different regions. They also question calibration of the molecular clock assuming a Gondwanan origin for the family, in contrast to a North American origin in the Paleocene (Weeks et al., 2005), and then using the separation of Africa from South America (95–100 Ma) to date the common ancestor of disjunct *Commiphora* and calibrate divergence times across the family. The point is that either/or approaches, as in climate versus the bolide impact in the demise of the dinosaurs, climate (Guthrie, 2006) versus hunters (Martin, 2005) in the disappearance of the North American megafauna, vicariance versus dispersal in biogeography, molecules versus morphology in systematics, the tropics as cradle versus museum (rather than both; Jablonski et al., 2006; Marshall, 2006), or undue emphasis on orogeny in the origin of the tropical dry forest is inexplicably limiting. In each of the above examples, there is the luxury of multiple factors to be integrated into explanations that approach the intricacies of reality.

PLIOCENE (5.3 to ~2.6 MA)

Climatic trends are episodic, and temperatures during the Pliocene are no exception. Although the general drift was toward lower MATs, at about planktic foraminifera zone N19 (middle Pliocene, ~4 Ma) marine temperatures increased, marking the last time the Earth was significantly warmer than at present (by ~3.5° C). Climates were seasonal, with winter temperatures estimated 5.4° C warmer than at present, and summer temperatures about the same as now. CO_2 concentrations were near modern levels at ~350 ppmv (compared to the present 380 ppmv), sea levels were ~35 ± 18 m higher along the U.S. Atlantic coast, there was only seasonal ice in the Arctic Sea, and precipitation was increasing. By the end of the middle Pliocene, climates resumed the trend toward lower MATs (Ravelo et al., 2004) and drier, more seasonal precipitation.

In addition to fluctuating temperatures within the overall trend toward coolness, dryness, and greater seasonality, there were other events and processes occurring simultaneously that complicate reading the history of environmental change and the biotic response. These include the intense Neogene orogeny in central and southern Mexico, with its myriad of climatic and biological consequences, and the superimposed independent patterns of solar variation (see e.g., I: pp. 45, 56, 62, 65, 66, 72). Another event that is particularly important for interpreting floras preserved in coastal basins is upwelling. Although the cause is not well understood, slight variations in the rate of the Earth's rotation, changing sea surface temperatures and salinity concentrations (ocean water stratification), and alterations in the physical configuration of the ocean basin will cause or enhance the upward movement of cold bottom waters. Thus, in an interval of warming temperatures, increased upwelling may perpetuate cool conditions along the coast, while the cessation or reduction of upwelling may augment the effects of a general warming. The reverse may be true during cooling trends, so the consequences can be to locally enhance, reduce, cancel out, or reverse the effects of other climate-forcing mechanisms. Just as redeposition is a bane to the interpretation of lacustrine, deltaic, and continental shelf floras, and as basin assemblages may reflect hydrologic changes due to

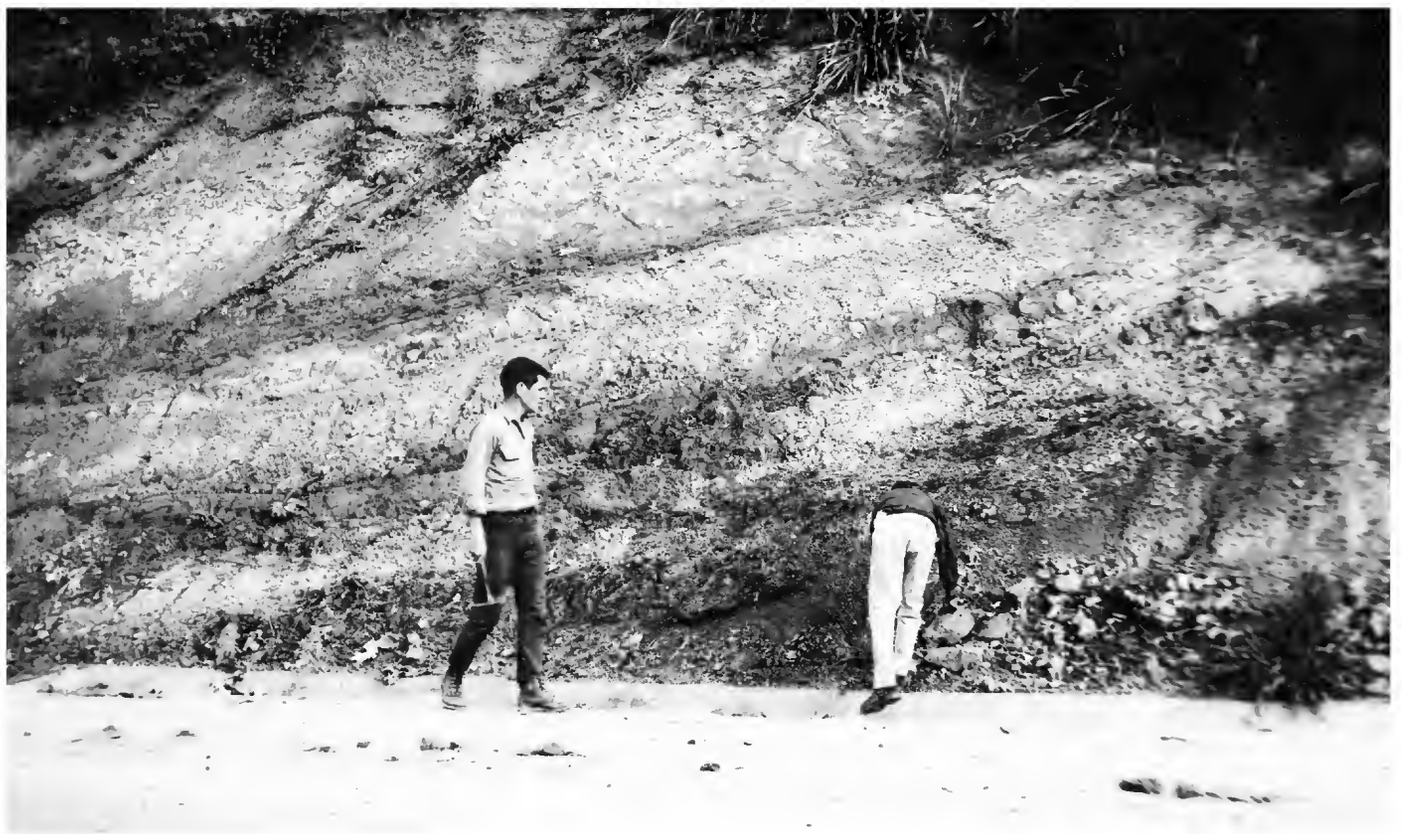


Figure 4.12. Roadside exposure of the middle Pliocene Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico.

tectonic events and isolation from regional or global trends, upwelling is often an additional complication for floras deposited along the coast. It was toward the end of the mid-Pliocene warm interval that the Paraje Solo flora was being deposited on the southeast coast of Mexico (Fig. 4.12; Graham, 1976a). Correlation charts compiled by PEMEX originally placed the Paraje Solo Formation in the Miocene, but it is now dated as middle Pliocene on the basis of planktic foraminifera (Akers, 1979). The composition of the microfossil flora is given in Table 4.1, the modern vegetation of Veracruz is summarized in Chapter 3, and the differences are discussed below.

The microfossils of the Paraje Solo flora are well preserved and exceptionally diverse (>100 taxa identified from among ~150 morphologically distinct palynomorphs; Figs. 4.13–4.33). A difference immediately apparent from the older floras is the modern aspect of the assemblage. For example, pollen of the family Asteraceae (Fig. 4.26) appears in the Oligocene (possibly in the Eocene; Chapter 8), but it does not become frequent or abundant until the Miocene in the Gulf of Mexico–Caribbean region (Graham, 1996). Highly ornate pollen of the family known in the stratigraphic literature as *Fenestrites spinosus* (Fig. 4.27), belonging to the tribes Lactuceae and Vernonieae, does not appear until the late Miocene and Pliocene. Similarly, chenoams (Fig. 4.25), although possibly present from the Cretaceous–Paleocene, are most abundant in the late Neogene. There is good representation of several Asteraceae types, including *Fenestrites*, along with chenoams in the Paraje Solo flora. In contrast, the mangrove *Pelliceria*, now distributed in Central America and northern South America and present in the Oligo–Miocene Simojovel flora, disappeared from its northernmost extent by Paraje Solo time, and the mangrove plant formation consists instead of *Rhizophora*, *Laguncularia*, and probably *Hibiscus tiliaceus* and *Acrostichum aureum*, as in the modern flora.

Modern lineages make for modern communities, and many close analogs of the middle Pliocene Paraje Solo plant formations are found in the present-day vegetation of Veracruz. The estimated paleocommunities of the Paraje Solo flora are given in Table 4.2, and they are arranged in Fig. 4.34 according to the modern vegetation types discussed in Chapter 3 (see also Fig. 3.53). The dry formations of desert and shrubland/chaparral–woodland–savanna are not evident in the flora, but this does not preclude their presence elsewhere in Mexico by the middle Pliocene. Rather, their local absence is likely due to the humid coastal environment and moisture provided by the northeast trade winds. The mangrove formation was well represented, as noted above, with *Rhizophora* pollen reaching 96% in some samples. This is expected in a Neogene flora deposited under warm-temperate to tropical, coastal environments.

The lowland Neotropical rain forest—What was not expected was the poor representation to absence of the lowland Neotropical rain forest in a fossil assemblage where there was sheet flow during the rainy season, rivers and wind throughout the year, and where hurricanes delivered spores and pollen into the depositional basin. In the modern vegetation, the rain forest occurs adjacent to the basin immediately inland to the mangrove formation. Nor is the Neotropical rain forest particularly well-represented in the Paleogene of Mexico generally, even at this time of widespread tropical environments. Part of the reason is that the principal source of Neotropical rain forest taxa for Mexico is South America. Wendt (1993) has shown that ~75% of the tropical canopy trees have South American affinities. In the early Eocene, South America was a near-island continent, still connected to Antarctica through the Drake Passage, and located about halfway between Africa and its present position. Furthermore, as South America came closer to North America in post–early Eocene times, MATs were declining and climates globally were becoming less tropical. Although climates per se were suitable for the development of a Neotropical rain forest in the lowlands of Mexico through about the early Miocene, a physical barrier to the principal source of tropical elements was in effect, and by the time the Panama land bridge was fully operative at ~3.5–3.1 Ma, climates were becoming more temperate. Prior arrival of Neotropical rain

forest elements favored those with the potential for drift or long-distance migration from South America, or they were descendants of earlier migrations from the Old World across the northern land bridges. Another factor limiting representation of the rain forest in the Paraje Solo flora is that before the onset of full glacial conditions, sea levels were higher and parts of the lowland were inundated to the base of the mountain slopes. This restricted lowland Neotropical rain forest habitats, and brought the shoreline closer to the wet phase of the lower to upper montane broad-leaved forest formation.

In the Neogene, the Earth's biotas were affected generally by cooling temperatures. If cooler climates affected the Paraje Solo vegetation, features related to this should be evident. One difference between the Pliocene and the modern flora is the presence of *Picea* (spruce) in the fossil assemblage. The closest stands of *Picea* today are to the north in the Sierra Madre Occidental (*P. mexicana*, or *P. engelmanii* var. *mexicana*, in Coahuila, Nuevo León; *P. chihuahuana* in Chihuahua, Durango) at elevations between ~2500 and 3500 m. Also, the mid-elevation deciduous forest association, and even the high-elevation montane coniferous forest association (e.g., *Abies*) are well represented, suggesting a downward shift in ecotones bringing these communities closer to the lowland basin of deposition. *Podocarpus* (Fig. 4.17) is another a member of the mid-elevation montane forest. *Podocarpus* occasionally occurs in the lowlands, probably as a relict of cooler times, but throughout its range it is predominantly an upland temperate element. The present annual temperatures at Coatzacoalcos average between 22° and 26° C (minimum 10° C), and annual rainfall is 3000 mm and more or less uniform (10%–18% winter rains, February through April). The most parsimonious interpretation of the collective evidence is that cooler climates prevailed at the Paraje Solo site, and that if this were during a time of overall mid-Pliocene warmth, upwelling is a plausible explanation. The net effect of isolation from a major source of tropical species, restricted lowland habitats, and changing Neogene and Quaternary climates trending toward cooler conditions was a limited lowland Neotropical rain forest that fluctuated in range and composition over time, with the modern version being a recent middle Pliocene and later innovation. Near the time the Paraje Solo study was published, investigations of the modern Neotropical biota and some geologic evidence were challenging the conventional wisdom that the rain forest and tropical environments remained mostly unchanged through long periods of Cretaceous and Cenozoic time (Vuilleumier, 1971). The Paraje Solo flora provided the first direct paleobotanical documentation that in an area where tropical rain forest is climax today, rain forest did not exist in the relatively recent geologic past (Chapter 8).

The presence of aquatic vegetation in the Paraje Solo flora is indicated by *Ceratopteris* and *Utricularia* (Fig. 4.29), and the possible presence of a beach/strand/dune community is suggested by pollen of *Acacia*, *Casearia*, *Coccoloba*, *Iresine*, *Terminalia*, and *Tournefortia* (Fig. 4.24). Pollen of the Poaceae (Fig. 4.21) reaches maxima of 27%, 29%, 30%, and 45% in some samples and, based on the overall composition of the paleoflora, these levels probably reflect a herbaceous reed-sedge marsh (tule/carrizal) or a saline grassland association of the freshwater herbaceous bog/marsh/swamp formation. Another plant formation well represented in the flora is the lower to upper montane broad-leaved forest, and this time, as opposed to the comparatively undifferentiated forests of the Oligo–Miocene Simojovel flora, there is a distinct association of northern temperate elements—*Pinus* (Fig. 4.20), *Alnus*, *Ilex*, *Juglans*, *Liquidambar*, *Myrica*, *Populus*, *Quercus* (Fig. 4.28), *Smilax*, and *Ulmus* (Fig. 4.33). A pine-oak association was probably present, although in plant microfossil assemblages the species of *Pinus* and *Quercus*, both found in other associations, cannot be distinguished. There is evidence for a high-altitude coniferous forest in the presence of *Abies* (Fig. 4.18), *Picea* (Fig. 4.19), and *Pinus* (Fig. 4.20). The highest altitude communities above timberline in the eastern Transvolcanic Belt are too far removed from the coastal basin of deposition, and the level to which such important components as Cyperaceae (Fig. 4.22), Poaceae (Fig. 4.21), Juncaceae, Caryophyllaceae, Asteraceae, Brassicaceae, Ranunculaceae, Rosaceae, and Apiaceae can be identified from pollen (mostly to family) precludes assessing the presence of páramo species.

Another Late Tertiary flora is from the region of Santa María Amajac north of Pachuca in Hidalgo (20°18'18"N, 98°42'44.4"W). In contrast to the Paraje Solo flora deposited along the coast at sea level, the Santa María Amajac flora grew along the margin of a lake situated in the north-central Transvolcanic Belt between the Sierra de Pachuca and the Sierra Madre Oriental. The present elevation is 1900 m (Aguilar & Velasco de León, 2002). The fossils came from the Atotonilco El Grande Formation, considered late Pliocene to Pleistocene in age by Segerstrom (1961). There are no radiometric dates directly from sediments containing the flora, but fission track dates of 4.2 ± 0.3 Ma and $^{40}Ar/^{39}Ar$ dates of 4.57 ± 0.02 Ma are available from rocks in the vicinity, and Aguilar and Velasco de León (2002) consider the flora to be Pliocene in age.

Although the composition of the flora is not well known (*Platanus*, *Quercus*, Rosaceae, Salicaceae are noted), the study is of interest because climate conditions were reconstructed on the basis of leaf physiognomy using the CLAMP program. The initial results were a MAT of 16.7° ± 1.2° C (compared to the modern 16.9° C), and a MAP of 650 ± 120 mm (modern 458.5 mm). The closer the flora is in age to the late Pliocene, the cooler it should be compared to modern interglacial times, especially at a paleoelevation nearing 1900 m. The authors attribute the similarity in MATs to the presence of a lake that buffered the surroundings against temperature extremes. The higher MAP is more difficult to explain, but it is generally agreed that CLAMP estimates are more precise for MAT than for MAP. The results are tentative, but it is a worthy beginning, and other Tertiary megafossil floras are available for analysis from Mexico. Recall (I: pp. 122–128) that identification of the specimens is not necessary for paleoclimate estimations based on LMA and CLAMP analysis.

Overall, the Late Cretaceous through Eocene vegetation of

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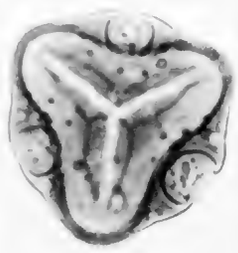
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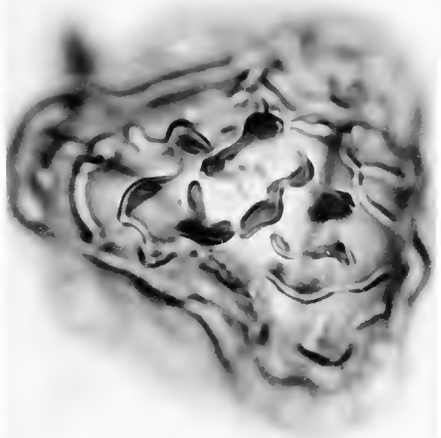
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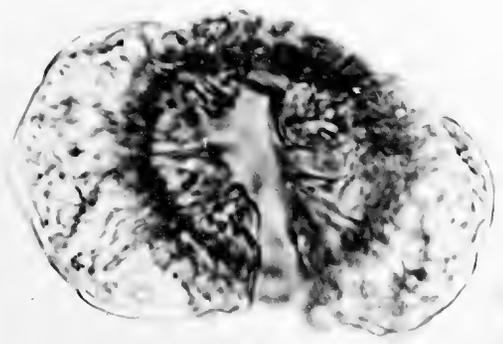
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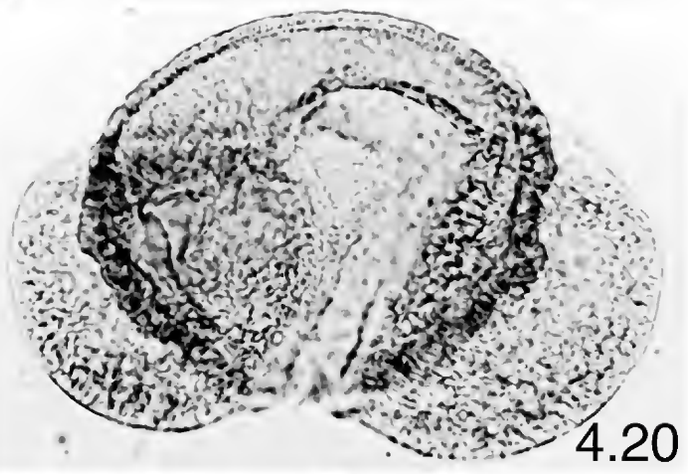
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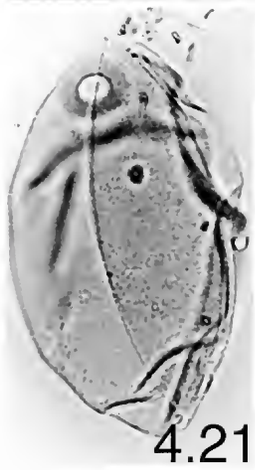
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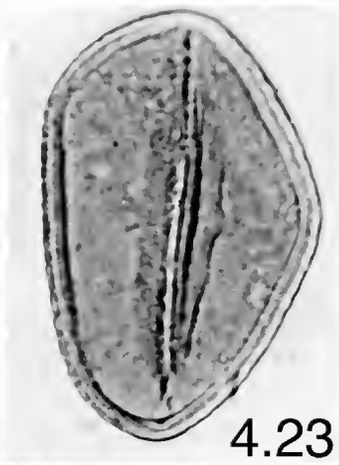
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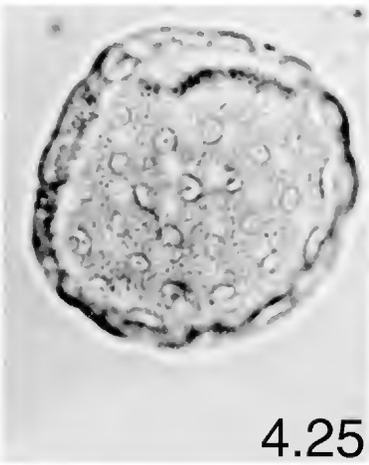
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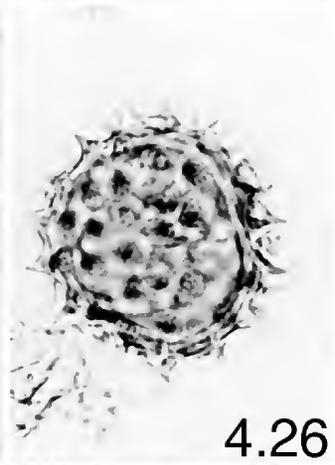
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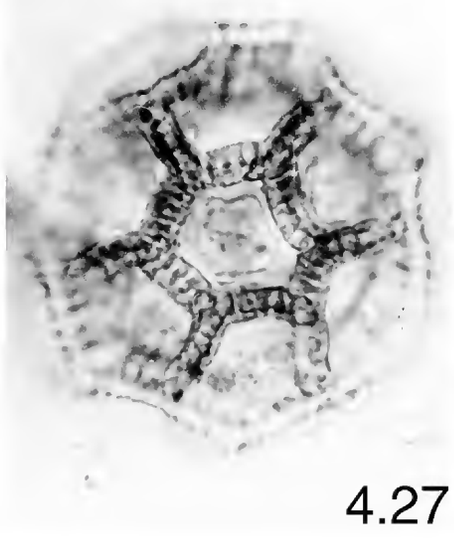
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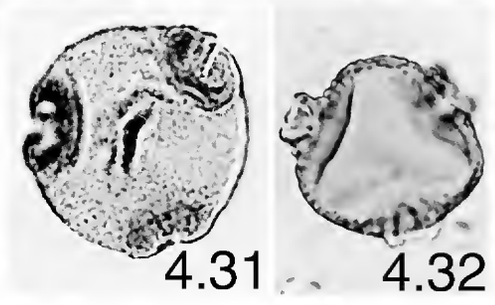
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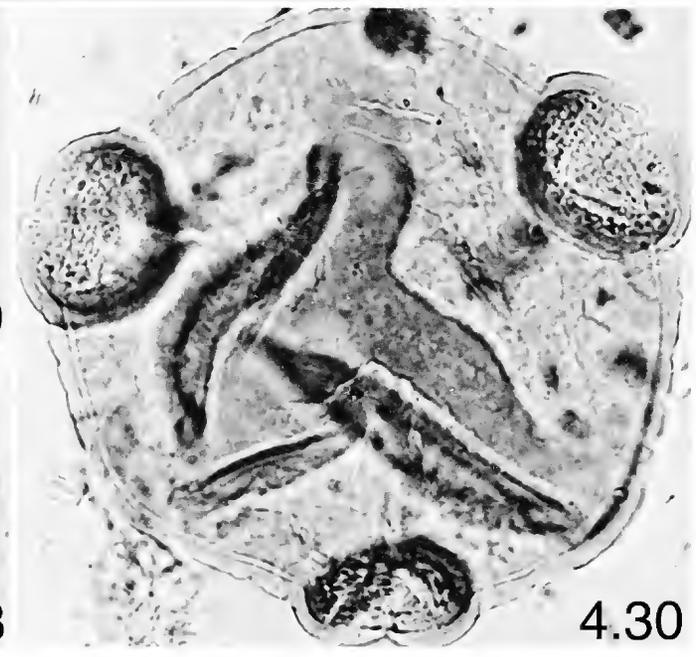
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Figures 4.13–4.33. Plant microfossils (spores and pollen) from the middle Pliocene Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico. 4.13. Monolete fern spore (smooth to nearly smooth forms are known in the stratigraphic literature as *Laevigatosporites*). 4.14. Monolete fern spore (*Verrucatosporites*). 4.15. *Cnemidaria–Hemitelia.* 4.16. *Pteris.* 4.17. *Podocarpus* (recognizable, in part, by the bulbous air sacs large in relation to the body of the grain). 4.18. *Abies* (thick apical cap). 4.19. *Picea* (lack of a re-entrant angle between the body and air sacs). 4.20. *Pinus* (marginal flange on either side of the body). 4.21. Gramineae (monoporate with annulus surrounding the pore; *Monoporites annulatus*). 4.22. Cyperaceae (wedge shape). 4.23. Palmae. 4.24. *Tournefortia.* 4.25. Chenoam (Chenopodiaceae–Amaranthaceae). 4.26. Compositae, *Echitricolporites.* 4.27. Compositae, Vernonieae–Lactuceae type, *Fenestrites.* 4.28. *Quercus.* 4.29. *Utricularia.* 4.30. *Ludwigia* (Onagraceae). 4.31. *Faramea* (triporate form, there are also diporate forms; Rubiaceae). 4.32. *Buettneria* (Sterculiaceae). 4.33. *Ulmus.*

Mexico reflects ancient communities with numerous genera and species distinct from modern ones, living in an environment of low physiogeographic relief, high sea levels, widespread maritime climates, warm temperatures, moderate rainfall, and little seasonality (La Misión, Rosario, Huepac Chert, Olmos, Piedras Negras, Laredo, Burgos Basin, El Bosque, La Trinidad floras). An ancient mangrove formation that included *Nypa* was present by the Eocene, and a near-modern version was present by the middle Eocene. The Oligocene and early Miocene was a time of transition from these conditions and floras to the presence of mostly modern taxa at the generic level, the beginnings of greater physiographic relief, more extensive continental climates, and greater seasonality in temperature and rainfall (Pie de Vaca, San José de Carmen, Palomares, Mint Canyon, and Simojovel floras). The lower to upper montane broad-leaved forest with many subtropical to warm-temperate components was present by the Oligocene, with an association of northern temperate elements appearing primarily in the middle Miocene and later. Grassland and shrubland/chaparral–woodland–savanna, as formations, developed in middle Miocene and later times. By the Pliocene, the taxa were modern at the generic level, Asian exotics had disappeared, and near-modern plant formations that included desert, a limited version of the lowland Neotropical rain forest, and probably early páramo, existed in an environment of significant physiographic relief and near-modern climates (Paraje Solo flora; Table 4.2).

The final phases in the modernization of the Mexican vegetation occurred with the turbulent climatic, tectonic, and volcanic events of the Ice Age, and with the appearance of agriculturalists. A detailed history of the Quaternary vegetation, consistent across the various basins, supported by independent lines of evidence, and correlated with climate-forcing mechanisms is just being assembled.

QUATERNARY (~2.6 MA–PRESENT)

Numerous factors alter patterns of plant and animal distribution by causing changes in climate (Chapter 1). One of the most important is the atmospheric concentration of greenhouse gases (CO_2, methane), but, as the amount of CO_2 declined from the waning of plate movement and associated volcanic activity after the breakup of Pangaea in the Jurassic and Cretaceous, a level was reached where other long-operating mechanisms became expressed. The Milankovitch variations are patterned changes in the position of the Earth relative to the sun, and these changes alter the amount of heat reaching the Earth's surface (insolation). The primary cycles follow periods of ~100,000 years (eccentricity; with a secondary period of ~400,000 years), 41,000–43,000 years (tilt), and 19,000–23,000 years (precession), euphemistically called stretch, tilt, and wobble (I: pp. 35–40). Cyclic deposits correlated with the Milankovitch variations are evident in ancient sediments (e.g., in the Triassic of the Newark Basin), but they are generally masked by other factors such as the amounts, trends, and fluctuations in atmospheric CO_2. By the Quaternary, however, the Milankovitch variations emerge as a clearly evident forcing mechanism for long-term climate change. After ~800 Kyr B.P., glacial cycles have followed the eccentricity variation rather than the previous 43-Kyr cycle, with some poorly understood mechanism for amplification, as changes in the shape (eccentricity) of the Earth's elliptical orbit alternately bring it closer to and farther away from the sun. The tilt cycle, which causes the greatest change in insolation, and

Table 4.2. Plant formations of the middle Pliocene Paraje Solo flora, Veracruz, Mexico. Several genera range through more than one community.

Desert—none
Shrubland/chaparral–woodland–savanna
Acacia, cf. *Brahea*, *Bursera*, *Casearia*, *Celtis*, *Combretum* (*Combretum–Terminalia*), *Comocladia*, *Cupania*, *Daphnopsis*, *Eugenia* (*Eugenia–Myrcia*), *Ilex*, *Laetia*, cf. *Malpighia*, *Mimosa*, cf. *Sapium*
Grassland
Gramineae
Mangrove
Large trilete fern spore (probably *Acrostichum aureum*, mangrove fern), *Hampea–Hibiscus* (probably *Hibiscus tiliaceus*), *Laguncularia*, *Rhizophora* (abundant)
Beach/strand/dune
Acacia, *Casearia*, *Coccoloba*, *Iresine* (a chenoam that can be recognized to genus), *Laguncularia*, *Terminalia* (*Combretum–Terminalia*), *Tournefortia*
Freshwater bog/marsh/swamp
Cyperaceae, Gramineae, *Bravaisia*, *Ludwigia*
Aquatic
Ceratopteris, *Utricularia*
Lowland Neotropical rain forest (no dominants)
Lycopodium, *Alchornea*, *Allophylus*, cf. *Astrocaryum*, *Bursera*, *Cedrela*, cf. *Chamaedorea*, *Faramea*, *Guarea*, *Gustavia*, cf. *Hiraea*, *Matayba*, cf. *Paullinia*, cf. *Protium*, *Sapium*, *Spathiphyllum*, *Symphonia*, cf. *Tetrorchidium*
Lower to upper montane broad-leaved forest
Alsophila, *Cnemidaria* (*Hemitelia*), *Cyathea*, *Lomariopsis–Stenochlanea*, *Lycopodium*, *Pityrogramma* (possibly *Anemia*), *Psilotum*, *Selaginella*, *Alchornea*, *Alfaroa/Oromunnea*, cf. *Bernardia*, *Cleyera*, *Dichapetalum*, *Hedyosmum*, *Ilex*, *Justicia*, *Liquidambar*, *Meliosma*, *Rajania*, *Securidaca*, *Serjania*, cf. *Stillingia*, *Struthanthus*
Temperate deciduous forest association—*Alnus*, *Juglans*, *Liquidambar*, *Myrica*, *Populus*, *Quercus*, *Ulmus*
Open (secondary, clearings)—*Dicranopteris*, *Alibertia*, *Borreria*, *Buettneria*, *Cuphea*, *Desmanthus*, *Passiflora*, *Rajania*, *Smilax*
Coniferous forest
Abies, *Picea*, *Pinus*, *Podocarpus*, *Quercus*

precession produce second-order effects within the 100,000-year pattern.

Since full glaciations set in about 2 million years ago in the north polar regions (slightly earlier in southern South America), cold intervals have constituted ~90% of the 100,000-year eccentricity periods, and interglacials have constituted ~10%. Air temperatures at the extreme glacial maxima are estimated at ~17° ± 1.8° C cooler than at present in the Northern Hemisphere (Bintanja et al., 2005). This has obvious implications for the proportion of time that different plant formations have occupied a region; e.g., the present desert formation in the north, and pine-oak associations at mid-elevations in many parts of Mexico. For ~90% of the past 2 Ma, these sites were occupied by, or were trending toward, woodlands and high-altitude coniferous forests of pines, bosque de oyamel (*Abies*), and *Picea*, respectively.

Within these intervals of cold glacial and warm interglacial periods induced by the extraterrestrial Milankovitch variations and mediated by other forcing mechanisms of terrestrial origin such as CO_2 concentration and ocean circulation, there were fluctuations. Among the most prominent was the Younger Dryas (after the European alpine plant *Dryas octopetala*; a cold interval between 12,800 and 11,500 years B.P.). This was a time of significantly lower temperatures as shown, for example, by a drop of 4°–6° C in surface ocean waters of the tropical southwestern Pacific (Gagan et al., 2000). The Younger Dryas resulted from a freshening of surface North Atlantic waters by melting glaciers that interfered with North Atlantic Deep Water formation and the northward transport of warmth by the conveyor belt (Tarasov & Peltier, 2005; Broecker, 2006). There was a less extreme but significant cold event at ~8200 years B.P. (Ellison et al., 2006) involving a drop of ~5° C for 200 years in the polar latitudes, and fluctuations at the PGCO (hypsithermal interval or xerothermic period) at 8000–6000 years B.P. There was a Medieval Warm Period between 800 and 1200 A.D., when the Vikings made extended sea voyages, including the colonization of Greenland and Newfoundland (but see Bradley et al., 2003). This was followed by the Little Ice Age, which lasted from (1300–)1580(–1850) C.E., one of the coldest in the last 12,000 years (MAT lower by ~1° C; North Atlantic by 3° C), during which the Vikings abandoned Greenland and Washington's troops suffered the severe winter at Valley Forge (I: pp. 278–279).

> "On the last day of 1607, Edmund Shakespeare [brother to William] was buried. It was a time of almost unbearable cold. By the middle of December the Thames had frozen solid so that 'many persons did walk halfway over the Thames upon the ice, and by the thirtieth of December the multitude…passed over the Thames in divers places.' A small tent city sprang up on the ice, with wrestling bouts and football matches, barbers' shops and eating-houses, trading upon the novelty of the silent and immobile river." (Peter Ackroyd, 2005, *Shakespeare, The Biography*, Nan A. Talese, New York. p. 457.)

A cycle operating on a time scale of a few to several thousand years are Heinrich events (seven in the past 100,000 years). These represent the culmination of cold intervals as revealed by layers of gravel on the floor of the North Atlantic as glaciers expanded and calved debris-laden icebergs into the ocean. They are now known from rock varnish patterns in the Great Basin, changes in the abundance of the marine alga *Florisphaera profunda* in the equatorial Atlantic Ocean (I: p. 40), and cold periods in Florida correlated with Heinrich events 1–4 (I: p. 283, fig. 8.9). D–O events occur on shorter cycles of several hundred to a few thousand years and may result from solar-forced input of freshwater into the North Atlantic Ocean (Braun et al., 2005). They have been reported from moraines in Chile, from sediments in Brazil, and on the Altiplano of Bolivia.

ENSO events date back at least 15 Kyr (Chapter 7, Ecuador), they probably operated throughout the Quaternary and middle to late Pliocene, and their effect on modern climate is documented in Latin America and elsewhere. For example, rainfall increases in northeastern Mexico during El Niños, and there are more cyclones along the Pacific coast.

Climate fluctuations and vegetation responses are particularly rapid at glacial–interglacial boundaries. There is typically a gradual buildup to glacial conditions, then a precipitous and chaotic drop into interglacial climates, a process Alley (2000) calls switches and dials. After the LGM at ~18 Kyr B.P., Greenland warmed by ~15° C in a decade or less at ~11,500 years B.P., and Leyden (1984) has documented this interval of climatic instability for Guatemala. As events and processes become better documented for the middle, lower, and high-southern latitudes, they constitute a background against which the very complicated record of Late Glacial and Holocene vegetation in Mexico and elsewhere can be viewed.

THE PEOPLING OF LATIN AMERICA

> "It was at some moment in the Pleistocene that humanity crossed what the geologist-theologian Pierre Teilhard de Chardin called the Threshold of Reflection, when something in people 'turned back on itself and so to speak took an infinite leap forward. Outwardly, almost nothing in the organs had changed. But in depth, a great revolution had taken place…'." (McPhee, 1980)

Events other than climate change have affected vegetation. One of the most important was the appearance of humans, and particularly those that had taken that "infinite leap forward" as herders and agriculturalists, clearing the land with axe and fire, altering drainage patterns and soil characteristics, then abandoning the site to successional recovery superimposed on

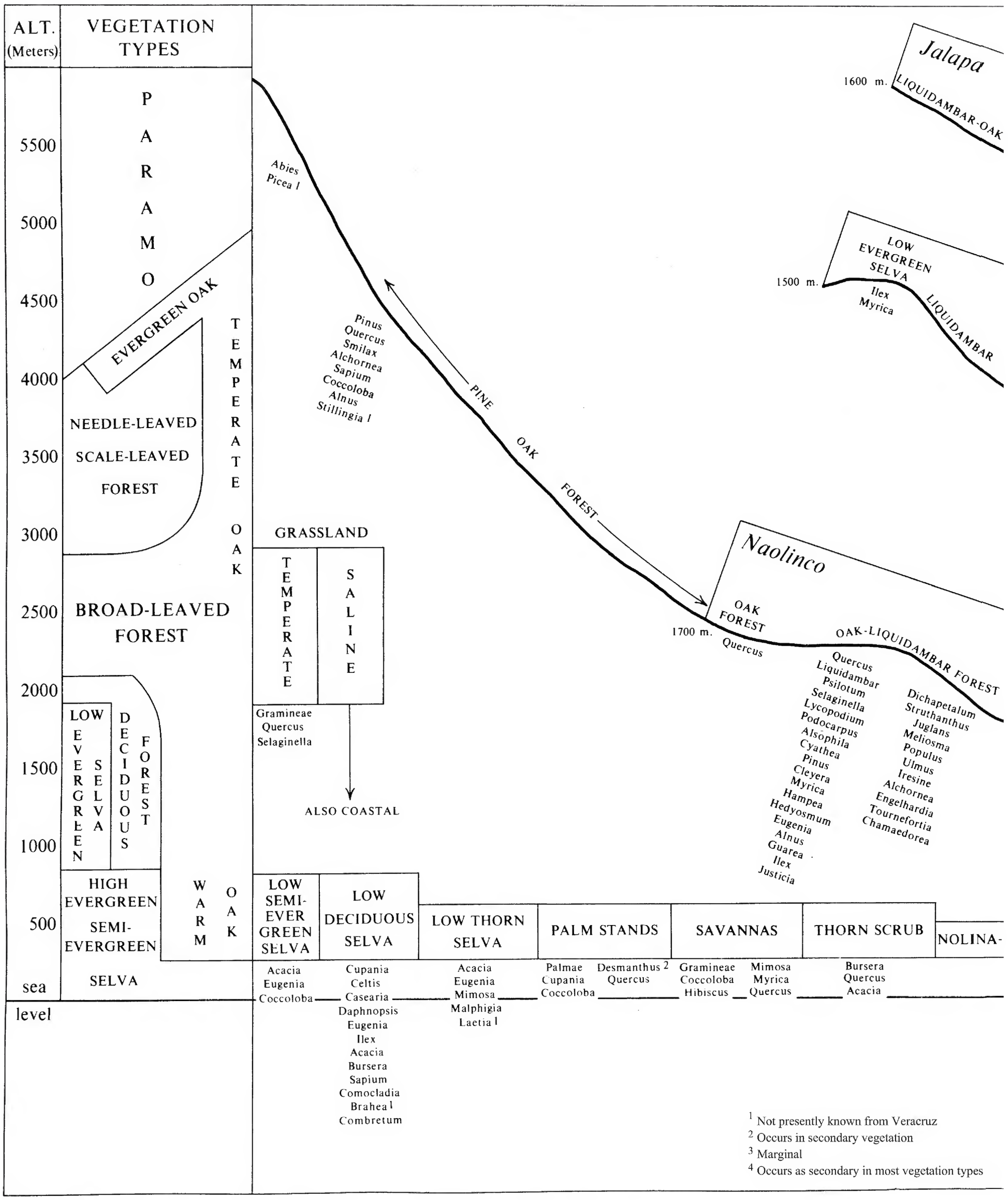
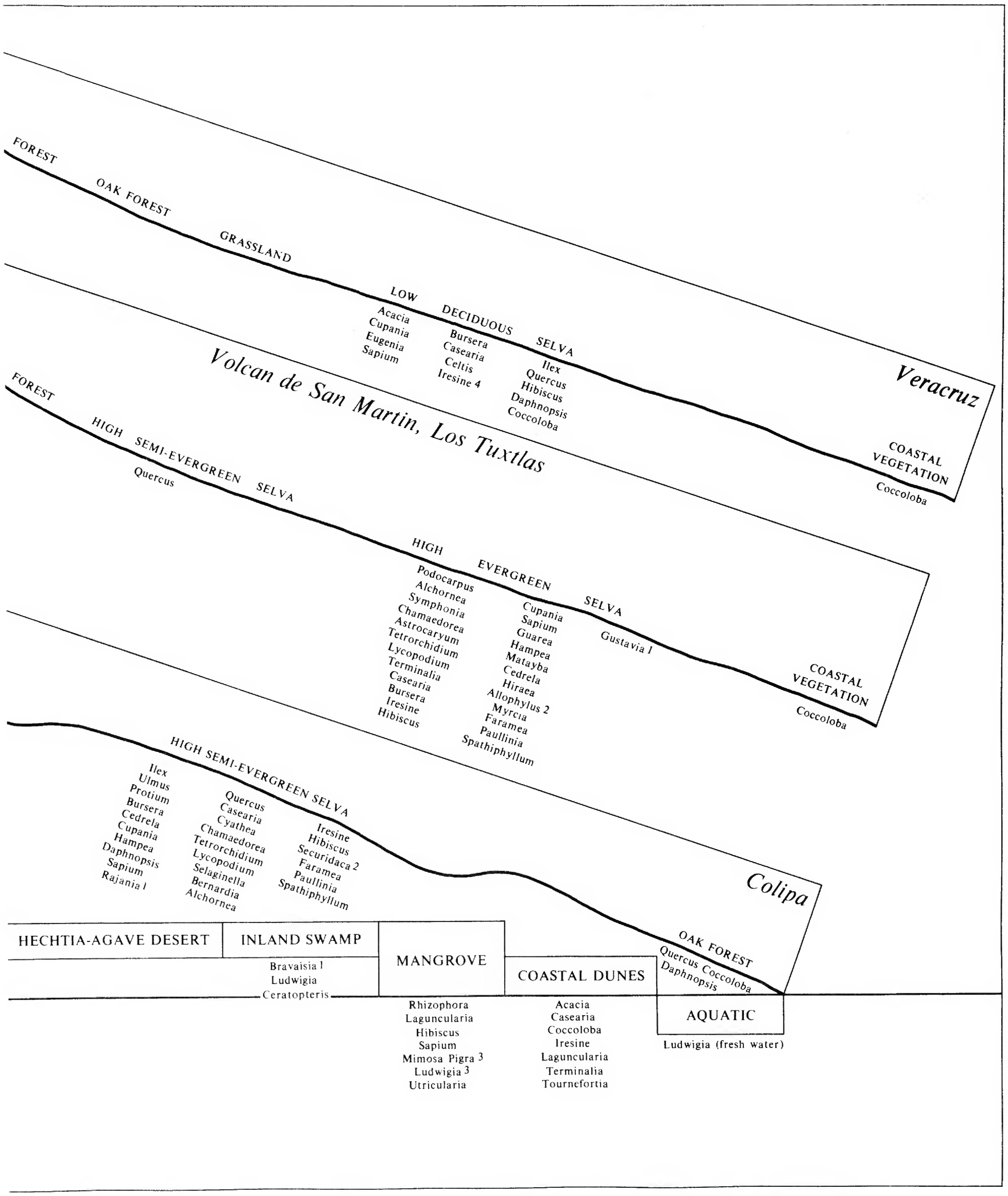


Figure 4.34. Distribution of taxa represented by fossil spores and pollen from the Paraje Solo flora (Graham, 1976a) arranged according to the modern plant formations of Veracruz, Mexico (Gómez-Pompa, 1973). (*Continued on next page.*)


Veracruz
FOREST
OAK FOREST
GRASSLAND
LOW DECIDUOUS SELVA
Acacia
Cupania
Eugenia
Sapium
Bursera
Casearia
Celtis
Iresine 4
Ilex
Quercus
Hibiscus
Daphnopsis
Coccoloba
COASTAL VEGETATION
Coccoloba
Volcan de San Martin, Los Tuxtlas
FOREST
HIGH SEMI-EVERGREEN SELVA
Quercus
HIGH EVERGREEN SELVA
Podocarpus
Alchornea
Symphonia
Chamaedorea
Astrocaryum
Tetrorchidium
Lycopodium
Terminalia
Casearia
Bursera
Iresine
Hibiscus
Cupania
Sapium
Guarea
Hampea
Matayba
Cedrela
Hiraea
Allophylus 2
Myrcia
Faramea
Paullinia
Spathiphyllum
Gustavia 1
COASTAL VEGETATION
Coccoloba
HIGH SEMI-EVERGREEN SELVA
Ilex
Ulmus
Protium
Bursera
Cedrela
Cupania
Hampea
Daphnopsis
Sapium
Rajania 1
Quercus
Casearia
Cyathea
Chamaedorea
Tetrorchidium
Lycopodium
Selaginella
Bernardia
Alchornea
Iresine
Hibiscus
Securidaca 2
Faramea
Paullinia
Spathiphyllum
Colipa
OAK FOREST
Quercus Coccoloba
Daphnopsis
HECHTIA-AGAVE DESERT
INLAND SWAMP
Bravaisia 1
Ludwigia
Ceratopteris
MANGROVE
Rhizophora
Laguncularia
Hibiscus
Sapium
Mimosa Pigra 3
Ludwigia 3
Utricularia
COASTAL DUNES
Acacia
Casearia
Coccoloba
Iresine
Laguncularia
Terminalia
Tournefortia
AQUATIC
Ludwigia (fresh water)

changes in vegetation due to climate. Disturbance also complicates the use of modern pollen rain studies in reconstructing pre-disturbance vegetation from microfossil assemblages. Often there are clear indications of early humans in an area, including shards and artifact fragments, an increase in the abundance of charcoal or charred organic fragments, zones of eroded sediments (sand or clay layers; e.g., the "Maya" clay in the Yucatán region), decrease in pollen of plants representing different ecotypes, decrease in the ratio of AP to NAP (viz., forest decline), appearance of cultivars such as *Zea mays* (Fig. 4.35) and manioc, and an increase in the pollen of weeds associated with cultivation (e.g., *Ambrosia*; Fig. 4.36). At other times, the early impact is difficult to detect, so it is worthwhile to know when humans entered a region and began modifying the vegetation—a period called the Anthropogene. The question involves the earliest introduction of humans into the New World, and when they entered Latin America and became agriculturalists.

The time of the initial introduction of northern Mongolian hunters into North America via Beringia is unsettled. The discovery of artifacts 30,000 years old in the Yana River Valley of Siberia (beveled foreshafts of spears carved from mammoth ivory and woolly rhinoceros horn; Pitulko et al., 2004) opens the possibility that humans moved into the New World along ice-free corridors prior to the LGM 20,000–25,000 years ago. Another site in European Russia at Mamontovaya Kurya, containing stone artifacts and a mammoth tusk with apparent cut marks, dates to 40,000 years ago. Unanswered questions are whether the hunters were year-round residents or only seasonal visitors to the northern steppe, and whether they were related to the Clovis people of Arizona (see below). Some artifacts (spears) are similar, and others (chipped stone cutters) are not. In contrast, Goebel et al. (2003) have new ^{14}C dates from Ushki Lake, Kamchatka, Russia, long considered an important site along the early migration route into the Americas. Rather than the previous age of ~17,000 years B.P., the new dates center around 13,000 years B.P. and are too recent to support pre-LGM introductions into the New World.

There is wide agreement that people of Mongolian ancestry crossed the Bering Strait in the Late Glacial by 15,000 years B.P. Some established the famed Clovis Site at Murray Springs, Arizona, by ~13,500 years B.P., regarded as the oldest locality containing confirmed evidence of humans in the New World. There is less agreement about older sites in northern North America (Hadingham, 2004) such as Bluefish Caves in the northern Yukon Territory (24,800 years B.P.) and Meadowcroft Rockshelter near Pittsburgh, Pennsylvania (16,000 to possibly 19,600 years B.P.).

In Latin America, stone tools, human bones, and associated *Mammuthus* remains from the Valley of Mexico have been dated at 24,040 ± 320 years B.P. and 21,700 ± 500 years B.P. (Romano, 1964; Mirambell, 1978; Garcia-Barcena, 1986). If so, this supports the early crossings through Beringia. A consensus is developing that Monte Verde in Chile dates from at least 12,500 years B.P. (Dillehay, 1989, 1997; see Gibbons, 1997),

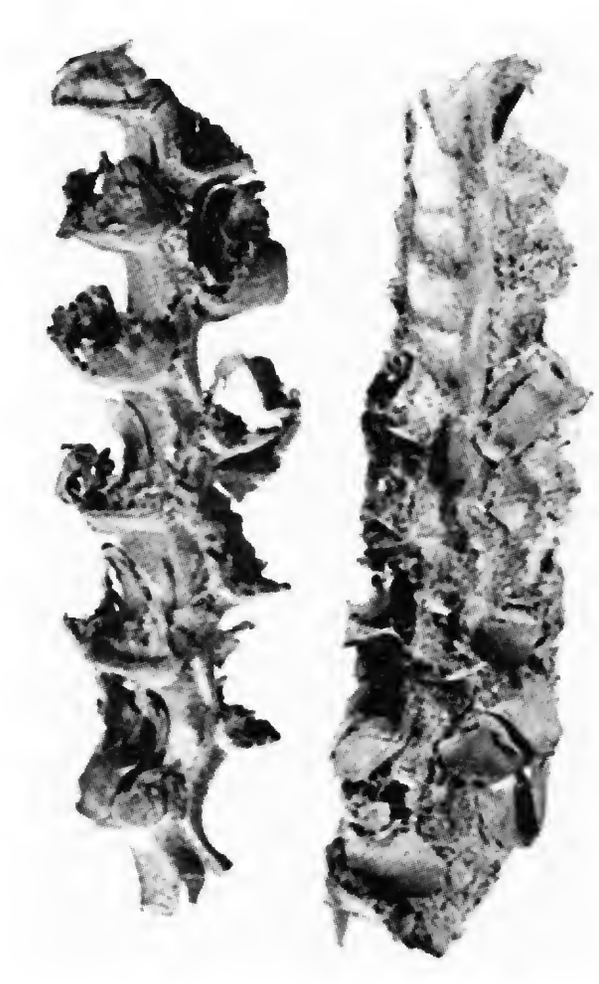


Figure 4.35. Corn cob remains ~6250 years old from Guilá Naquitz Cave, Oaxaca, Mexico. From Brown (2001); Piperno and Flannery (2001). Used with permission of Kent V. Flannery.

although there are other localities in Latin America thought to date from about 13,000 years B.P. such as Taima-Taima in Venezuela, Tagua-Tagua in Chile, and Los Toldos Cave in Argentina (Lewin, 1987), and there are sites that are presumed older but with less settled chronologies. González et al. (2006) report human footprints in the Xalnene volcanic ash layer south of Puebla dated at >40 Kyr B.P. by OSL of incorporated baked lake sediments.

New evidence continues to emerge, but the picture is still far from clear. Ever since the popularized adventures of Thor Heyerdahl's 1947 *Kon-Tiki* expedition, the possibility has been entertained that people, other than northern Asians, arrived in the New World by boats and by routes other than Beringia. The 9300-year-old skull of the Kennewick Man from Washington State has craniofacial features interpreted as different from Native Americans and similar to an increasing number of remains now being found at other sites in the Americas. González-José et al. (2003) believe the modern Pericú group of southern Baja California is a separate lineage of ancient Americans with southern Asian rather than Mongolian ancestry. It is too early to speculate on when and how the ancestors of the Pericú arrived in Mexico, but the evidence suggests that, as expected, the origin of humans in the New World is probably more complex than just the migration of northern Asians across Beringia at the end of the last glacial.

Views about the first agriculturalists in Latin America are also changing. It has long been advocated that sedentary populations first began clearing land and planting crops, particularly *Zea mays* (corn), in the uplands of southern Mexico (the Valley of Mexico, the Valley of Oaxaca; Table 4.3), although

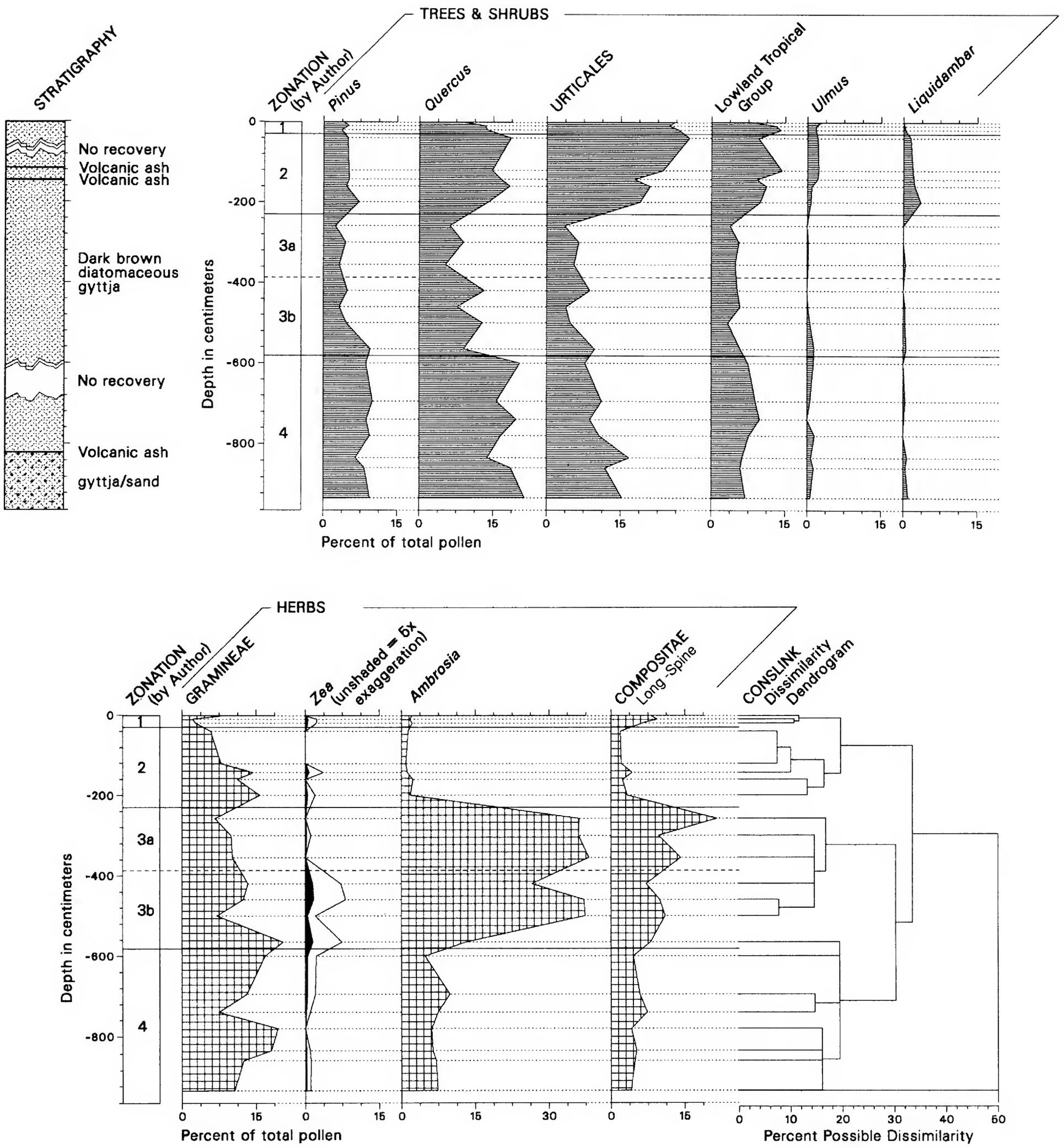


Figure 4.36. Spore and pollen diagram from Lago Catemaco, Veracruz, Mexico. Note the decrease in all tree genera (top diagram) and the simultaneous increase in *Zea*, other grasses, *Ambrosia*, and other composites (bottom diagram). From Byrne and Horn (1989). Used with permission of the American Association of Stratigraphic Palynologists Foundation, Dallas.

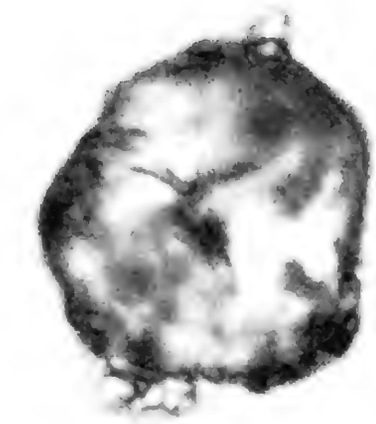


Figure 4.37. Starch grain of manioc (22 μm) from grinding stone, Aguadulce Rock Shelter, Panama. Reprinted from Piperno and Pearsall (1998), Academic Press, used with permission of Elsevier Science Publishers, Amsterdam.

the chronological control was not exact. These populations were then thought to have spread southward along grassy and sparsely vegetated coastal areas into the lowlands. It now appears that agriculture began at about the same time, perhaps even a little earlier, in the lowlands (Piperno & Pearsall, 1998; Piperno & Flannery, 2001; Pope et al., 2001). In addition to tools and pottery, charcoal, erosion layers, plant debris, evidence of forest clearance, and spores and pollen of cultivars and weeds, evidence of agriculture now includes phytoliths and starch grains. Phytoliths (I: pp. 121–122; Piperno, 2006) can preserve in soil and lake sediments, and both phytoliths and starch grains (Fig. 4.37) are distinctive microstructures that can remain on pots, utensils, and dental material. Combining the archeological and phytoarcheological evidence, it appears likely that humans began having some impact on vegetation in Latin America by 15,000 years B.P.; locally more intensive land modification began at least 12,000 years B.P.; and some morphological changes in seed and phytolith size suggest plant domestication by ~9000–8000 years B.P. and cultivation by 7000 years B.P. (Bush et al., 1989). Markgraf (1989) notes that after 6000 years B.P., paleovegetation changes can no longer be ascribed automatically to climate alone.

The extent to which early humans modified the landscape has led to the question of whether this modification eventually contributed to the demise of the civilization itself. Population centers located in marginal environments have always been susceptible to changes in climate that could alter the balance between sustainability and collapse. The early lowland Maya, subsisting on the karst topography of the Yucatán Peninsula, contended with limited amounts of water in return for open and less competitive habitats, and a considerable part of their energies were devoted to designing, constructing, and managing hydrological systems to conserve water (Matheny, 1976). The supply of water fluctuated over time, so the Maya kept records in an effort to anticipate shortages by forecasting climatic change (Folan & Hyde, 1985). However, sometimes a series of events or a combination of factors occurs that exceeds the will and technology of the people or the carrying capacity of the land. For the Maya (Fig. 4.38) this began with forest clearance and soil erosion ~1700–850 years B.P. (Rosenmeier et al., 2002) and culminated with the droughts of the Medieval Warm Period ~900 years B.P.

The climate of the region has been reconstructed from ^{18}O values and sediment records (gypsum-calcite) on the Yucatán Peninsula of Mexico (Hodell et al., 1995; Curtis et al., 1996; see also Yucatán Peninsula, this chapter; Guatemala, Chapter 6). The records show low values (wet conditions) from ~3310 to 1785 ^{14}C years B.P.; high values (dry conditions) between 1785 and 930 ^{14}C years B.P. with especially dry climates around 1171, 1019, and 943 ^{14}C years B.P. (862, 986, and 1051 A.D.); then a prolonged drought between 750 and 850 A.D. A new core from Yucatán with faster sedimentation rates has been dated more closely, allowing analyses of every six- to seven-year interval of the 2600-year record, and droughts are evident about every 208 years (Hodell et al., 2001). At another site, in the Cariaco Basin of northern Venezuela, the titanium content of the sediments indicates fluctuations in river input reflecting an extended dry period, punctuated by exceptionally dry intervals of three to nine years, during the Maya Terminal Classic Period (Haug et al., 2003; Fig. 4.39). The cause of the drought may have involved the 210-year cycle in solar activity (Braun et al., 2005), as revealed by cores from the North Atlantic and by increased ^{14}C preserved in tree rings, which produces greater warmth and a smaller P/E ratio. The Maya civilization collapsed around 900–750 A.D.

THE NORTHERN DESERTS

Interglacials bring desert climates to the lower elevations of northern Mexico. One reason for this is that the flow of the northern jet stream places the Bermuda–Azores

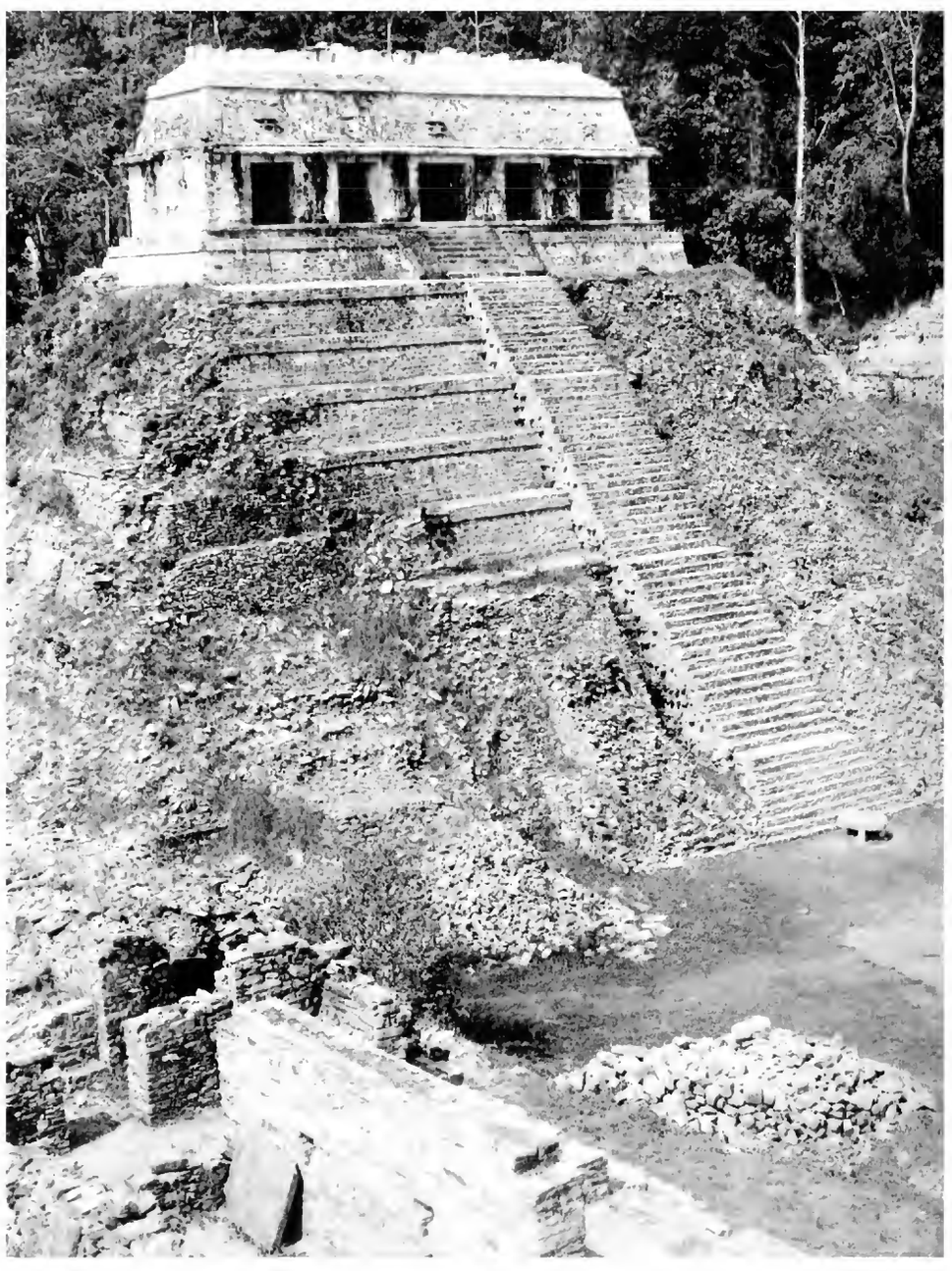


Figure 4.38. Main pyramid, Chichén Iztá (Maya), Yucatán, Mexico.

Table 4.3. Reports of evidence for early occupation and ancient agriculture in Latin America. Dates are as cited by the original authors/reviewers. Cal. = calendar.

Site/occupation–crop	Age	Reference
Mexico		
San Andrés, Tabasco		
Cultivated *Zea* (corn), forest clearing	5100 cal. years B.C. (6200 ^{14}C years B.P.)	Pope et al., 2001
Domesticated *Zea mays*	5000 cal. years B.C. (6000 years B.P.)	
Manihot (manioc)	4600 cal. years B.C. (5800 years B.P.)	
Helianthus (sunflower)	2500 cal. years B.C. (4000 years B.P.)	
Gossypium (cotton)	2500 cal. years B.C. (4000 years B.P.)	
La Venta, Tabasco, Olmec settlement	1750 B.C.	Rust & Sharer, 1988
Laguna Catarina, Veracruz		
Zea mays	4100 years B.C.	Sluyter, 1997
Lago Catemaco, Sierra de los Tuxtlas	~3000 B.P.	Byrne & Horn, 1989
Zea mays		
Guilá Naquitz Cave, Valley of Oaxaca		
Zea mays (cobs)	6250 cal. years B.P. (5400 ^{14}C years B.P.)	Piperno & Flannery, 2001
Cucurbita pepo	~9000 ^{14}C years B.P. 6250 cal. years B.P. (5400 ^{14}C years B.P.)	Smith, 1997
Lake Pátzcuaro, Michoacán (accelerated soil erosion)	3500 ^{14}C years B.P.	O'Hara et al., 1993
West Indies		
Caribbean region, hunters-foragers	~5000–4000 years B.P.	Meggers & Evans, 1983
Central America		
Belize		
Colha		
Deforestation	3400 B.C.	Jacob & Hallmark, 1996
Theobroma cacao (chocolate)	600 B.C.	Hurst et al., 2002
Guatemala		
Petén, Maya occupation	3000 B.P.	Binford et al., 1987
Honduras		
Lake Yojoa, slash-burn, *Zea*	~4500 years B.P.	Rue, 1987
Costa Rica		
La Selva		
Zea mays	2700 years B.P.	Kennedy & Horn, 1997
Panama		
Aguadulce Shelter, Pacific Coastal Plain	7000–5000 B.P.	Piperno et al., 2000
Starch grains		
Dioscorea (yam)		
Manihot esculenta (manioc)		
Maranta arundinacea (arrowroot)		
Zea mays		
Gatún Basin		
Zea mays	? (after 7300 B.P.)	Bartlett et al., 1969
South America		
Chile		
Atacama Desert, hunters-foragers	13,000 ^{14}C years B.P.	Dillehay, 2002 Núñez A. et al., 2002
La Venta, hunters-foragers	12,500 years B.P.	Dillehay, 1989, 1997
Atacama Altiplano, hunters-foragers	10,820 B.P.	Grosjean & Núñez A., 1994

Table 4.3. Reports of evidence for early occupation and ancient agriculture in Latin America. *(Continued)*

Site/occupation–crop	Age	Reference
Colombia		
Sabana de Bogotá, hunters-foragers	pre-12,000 years B.P. (El Abra Stadial)	Cooke, 1998
Venezuela		
Sabana de Bogotá, hunters-foragers	12,000–11,000 years B.P.	Cooke, 1998
Brazil		
Caverna da Pedra Pintada, Monte Alegre, Amazon, hunters-foragers *Astrocaryum vulgare* *Attalea microcarpa*, *A. spectabilis* *Bertholletia excelsa* (Brazil nut) *Byrsonima crispa* *Hymenaea* cf. *parvifolia*, *H. oblongifolia* *Mouriri apiranga* *Sacoglottis guianensis* *Talisia esculenta* *Vitex* cf. *cymosa*	11,200–10,000 ^{14}C years B.P.	Roosevelt et al., 1996 (see Letters, *Science* 274, Dec. 13, 1996)
Itaparica, Bahia, cerrado, hunters-foragers	9000 years B.P.	Klink & Moreira, 2002 (and references cited therein, p. 70)
Argentina		
Patagonian Andes, extra-Andean plains, hunters-foragers	3,000 ^{14}C years B.P.	Coronato et al., 1999
Los Toldos, extra-Andean Patagonia, hunters-foragers		Paez et al., 1999
Fell's Cave	11,000–10,000 years B.P.	
La Martita Cave	>8000 years B.P.	
Ecuador		
Southwestern Ecuador *Zea mays*	10,130–9320 ^{14}C years B.P. (12,000–10,000 cal. years B.P.)	Piperno & Stothert, 2003
La Emerenciana (coastal) *Zea mays*	4200 years B.P.	Staller & Thompson, 2002 (see Piperno, 2003)
Vargas site, Santa Elena Peninsula	>6000 B.P.	Pearsall, 2002
Zea mays	>6000 B.P.	Pearsall, 2002
Peru		
El Paraíso, cultivars *Equisetum* *Amaranthus* *Baccharis* *Canna edulis* *Capsicum* (pepper) *Cereus* *Cucurbita ficifolia*, *C. maxima*, *C. moschata* (squash) *Cyperus–Scirpus* *Furcraea* *Gossypium* (cotton) *Gynerium sagittatum* *Inga feuillei* *Lagenaria siceraria* (gourd) *Lucuma bifera* *Pachyrhizus tuberosus* (jicama) *Pennisetum* *Phragmites communis* *Phaseolus lunatus* (lima bean), *P. vulgaris* (bean) *Physalis* (tomatillo) *Prosopis* *Psidium guajava* (guava) *Rapanea* *Salix chilensis* *Sapindus saponaria* (soapberry) *Solanum* (potato) *Tessaria integrifolia* *Tillandsia latifolia* *Typha angustifolia*	1800 B.C.	Quilter et al., 1991

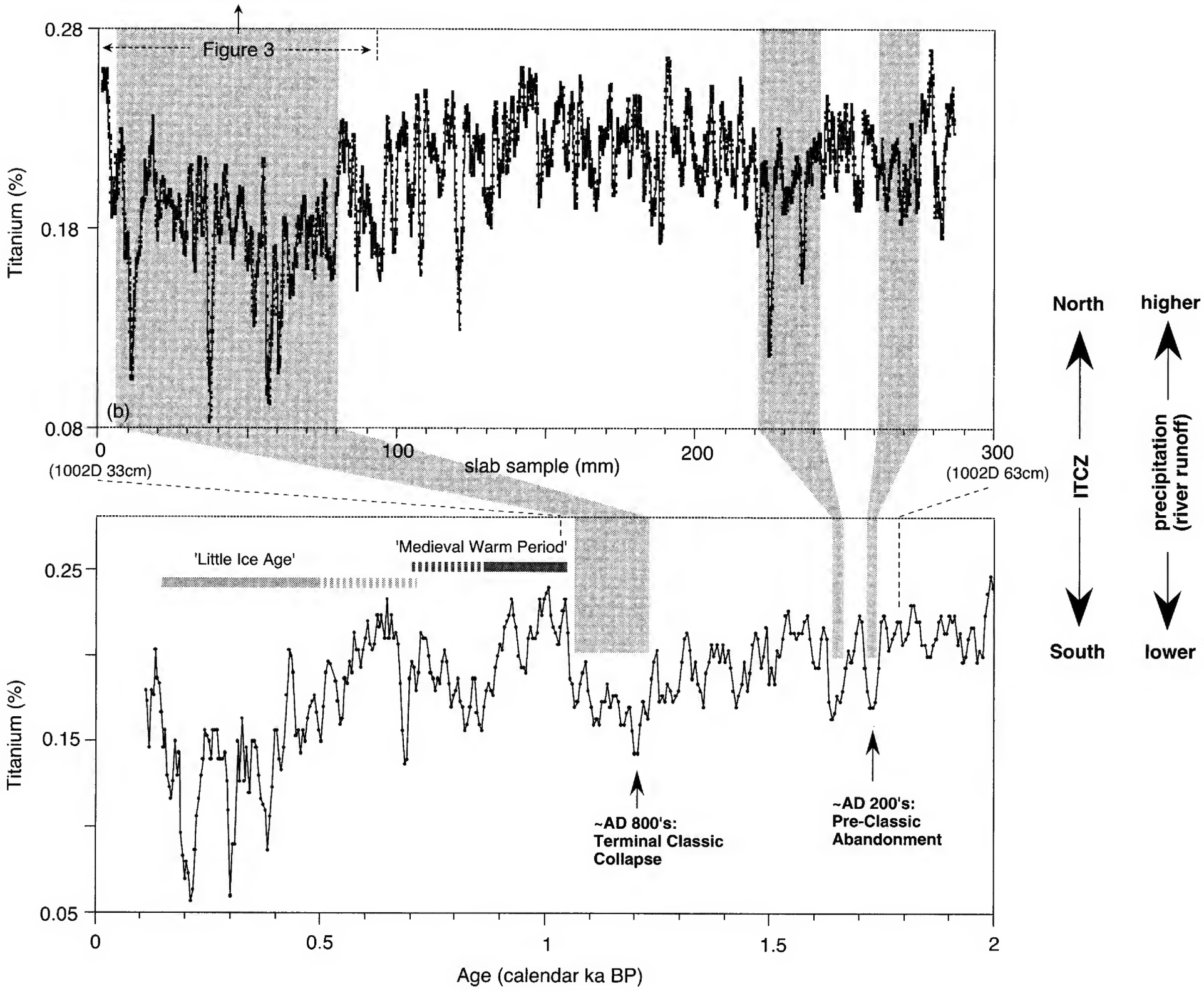


Figure 4.39. Top: Titanium content of sample from ODP hole 1002D, Cariaco Basin, Venezuela. Periods of drought are indicated by low titanium values and are likely the result of climate conditions preventing the northward movement of the ITCZ and associated rainfall. Bottom: Titanium content of sample from ODP hole 1002C, Cariaco Basin, for the past 2000 years, with timing of the Little Ice Age, Medieval Warm Period, Pre-Classic Maya abandonment of ceremonial centers, and Terminal Classic collapse. From Haug et al. (2003). Used with permission of *Science*.

high-pressure system (part of the Hadley circulation cell or subtropical high-pressure belt) at its present position. Conditions are quite different in glacial times. During each of the 18–20 maxima of the Pleistocene glaciations, the dome of the Laurentian ice sheet over Hudson Bay was about one mile thick. This mountain of ice divided the polar jet stream and deflected the southern arm southward weakening or displacing the Bermuda High. The mid-latitude westerlies moved southward and brought intervals of greater moisture (pluvial climates) to the region of northern Mexico (Brook et al., 2006; speleothem, Carlsbad Caverns, New Mexico), mostly in the form of increased winter rains. A packrat midden in the Sierra San Francisco, Baja California Sur, dated near the Late Glacial and Holocene transition (12,200 years B.P.), contains *Juniperus californica*. This species no longer grows there, but is found to the north in southern California. The MAT was an estimated 5°–6° C cooler than at present, with twice the winter precipitation (Rhode, 2002). Cycles of dry and moist climates within the last glacial are preserved in packrat middens in valleys of playa lakes in the Mexico–New Mexico borderland (Holmgren et al., 2003). At ~18–12 Kyr B.P. (16–10 Kyr ^{14}C years) the vegetation was *Pinus edulis* (pinyon pine)–*Juniperus scopulorum*–*J.* cf. *coahuilensis* (juniper) woodland. At the beginning of the Late Glacial (~9000 ^{14}C years B.P.) these declined and were replaced by drier oak-juniper woodland, and then by modern Chihuahuan Desert elements and climate regimes (~4000 ^{14}C years B.P.; e.g., *Larrea tridentata*, *Fouquieria splendens*; Chapter 2).

The many interactive components of climate are complex, however, and even the most powerful computers and sophisticated statistics have not yet produced a satisfactory model

for long-term climate change (I: vii–ix, ch. 2). To illustrate the point, the meandering of the Hadley convection cell described above is overlain by another set of related events. Winter precipitation is generated by westerly winds off the mid-latitude Pacific Ocean meeting another tropical monsoonal[2] system generated by the northeast trade winds, and the boundary is in northern Mexico (Metcalfe et al., 1997; Metcalfe, 2006). Changes in the relative strength and position of these two systems influence the amount and seasonal distribution of moisture carried across the northern deserts, and because they originate in separate geographic regions (the eastern Pacific and the Gulf of Mexico), they function somewhat independently, resulting in immensely complex patterns of precipitation. Superimposed on both these forcing mechanisms (the Hadley convection cell, and the westerlies–eastern monsoonal regime) are ENSO events that further perturbate the system. It is not surprising, therefore, that patterns of rainfall in the drylands of the Chihuahuan Desert and in the Sonoran Desert in the Late Glacial (12 Kyr B.P.) through the Holocene are not synchronous. For example, Spaulding (1991) interprets packrat midden evidence from Sonora as indicating dry mid-Holocene conditions at 7.5 to 4.7 Kyr B.P., while Van Devender (1985, 1990) believes more moist conditions prevailed in Chihuahua between 9 and 4.5 Kyr B.P.

Regardless of the complexity and the underlying causes, the overall result was widespread pluvial climates that converted much of the arid vegetation of northern Mexico to (or toward) shrubland/chaparral–woodland–savanna during each of the glacial maxima, and dry climates in the interglacials when the deserts were reconstituted. In the last cycle, a version of the Chihuahuan and Sonoran deserts was established ~12 Kyr B.P. at the end of the LGM, followed by progressively smaller fluctuations in precipitation toward Recent times that produced the modern deserts. Erosion terraces of Quaternary age are present along the forefront of the Sierra Madre Oriental (Ruiz Martínez & Werner, 1997), and these may eventually provide further information on the frequency, timing, and magnitude of the climatic fluctuations. Diatom records show that the moist intervals of the LGM extended to about the latitude of Lake Pátzcuaro (19°35'N) in the highlands of central Mexico (Bradbury, 1997).

The vegetation of northern Mexico during the Early Glacial advances (Nebraskan, Kansan, Illinoian in the classical chronology) and interglacials (Aftonian, Yarmouth, Sangamon) is poorly known, but conditions probably approximated those of the last and better-known Wisconsin–Holocene stages. A fauna of Irvingtonian land mammal age (early Pleistocene; I: pp. 98–106) is known from near El Golfo de Santa Clara in Sonora, Mexico, where a metacarpal of the giant anteater *Myrmecophaga tridactyla* was uncovered (Shaw & McDonald, 1987). Its present northern limit is 3000 km to the south in more moist climates of Central and South America. The Sangamon interglacial was warm, and some intervals were warmer than at present. Evidence for this is afforded by *Porites* and *Pocillopora* corals that ranged >300 km north of their present range in the Gulf of California and 600 km north along the Pacific coast (Muhs et al., 2002).

Pollen from two cores in the Cuatro Ciénegas Basin in Coahuila (elevation 740 m), with basal sediments dated >31,400 ^{14}C years, were earlier interpreted to mean that "vegetation ecologically equivalent, if not identical, to that now present has occupied the floor of the basin since mid-Wisconsin time," and surprisingly that "aquatic and terrestrial habitats of the valley lowlands remained stable environments throughout the Quaternary, regardless of fluctuations in regional climate" (Meyer, 1973, p. 982). Such long-term stability in climate and vegetation, even in basin settings, is not typical, and stasis to this extent is not evident in the vegetation from other parts of the desert (I: pp. 292–299). A study from the Alta Babicora Basin to the north (elevation 2200 m) shows increases in *Picea*, *Pinus*, and *Quercus* in the Late Glacial and conditions generally more mesic than at present (Metcalfe et al., 1997, 2002). Diatoms from the same site (>11 Kyr B.P.) indicate marked fluctuations in climate at the Pleistocene–Holocene transition and a lower MAP during the Younger Dryas chronozone. Plant remains from packrat middens (I: pp. 131–137) have been studied from Cañon de la Fragua, Puerto de Ventanillas, and the Sierra de la Misericordia in the Chihuahuan Desert of Coahuila. The vegetation in the late Wisconsin of *Juniperus* and *Pinus remota* woodland began changing toward Chihuahuan Desert vegetation at ~12,600–9000 years B.P. The Cañon de la Fragua is adjacent to the Cuatro Ciénegas Basin and rather than stable climates, the middens reflect greater MAP, cooler summers, and fewer winter frosts in the late Wisconsin than at present (Van Devender, 1990; Van Devender & Burgess, 1985). To the west in the Sierra Bacha along the coast of Sonora, plant remains from packrat middens indicate that the early Holocene was wetter and cooler than at present, due in part to upwelling. Among the plants identified are *Ambrosia dumosa*, *Bursera*, *Cercidium microphyllum*, *Larrea divaricata*, *Encelia farinosa*, *Ferocactus cylindraceus*, *Fouquieria columnaris* (boojum), and *Prosopis*. The middle Holocene was drier (Van Devender et al., 1994), it became even warmer and drier in the late Holocene (Anderson & Van Devender, 1995), and modern conditions are evident by ~4000 years B.P. (see also, for Sonora: King & Van Devender, 1977; Van Devender et al., 1990; for the Chihuahan Desert: Wells, 1966; Van Devender, 1985; Elias, 1992; Elias et al., 1995). In the San Felipe Basin of northeastern Baja California (17 in Fig. 4.2), the vegetation of the mid-Wisconsin included abundant *Pinus*, *Juniperus*, and *Artemisia* (i.e., woodland rather than desert; Lozano-García et al., 2002; Figs. 4.40–4.42). A similar sequence of moist conditions at the LGM, and switch and dial fluctuations trending toward increased seasonality and aridity later, also characterizes aeolian-lacustrine records from the Mojave Desert and the Great Basin of the southwestern United States (Tchakerian & Lancaster, 2002) and dune formation in Baja California Sur (Murillo de Nava et al., 1999). Evidence from stalagmites (Henderson, 2006), as in caves from central Texas (Musgrove et al., 2001), reveals increased moisture at ~71–60, 39–33, and 21–12 Kyr B.P. during the LGM (cool-wet). Growth was slower at times during the Holocene (15–12

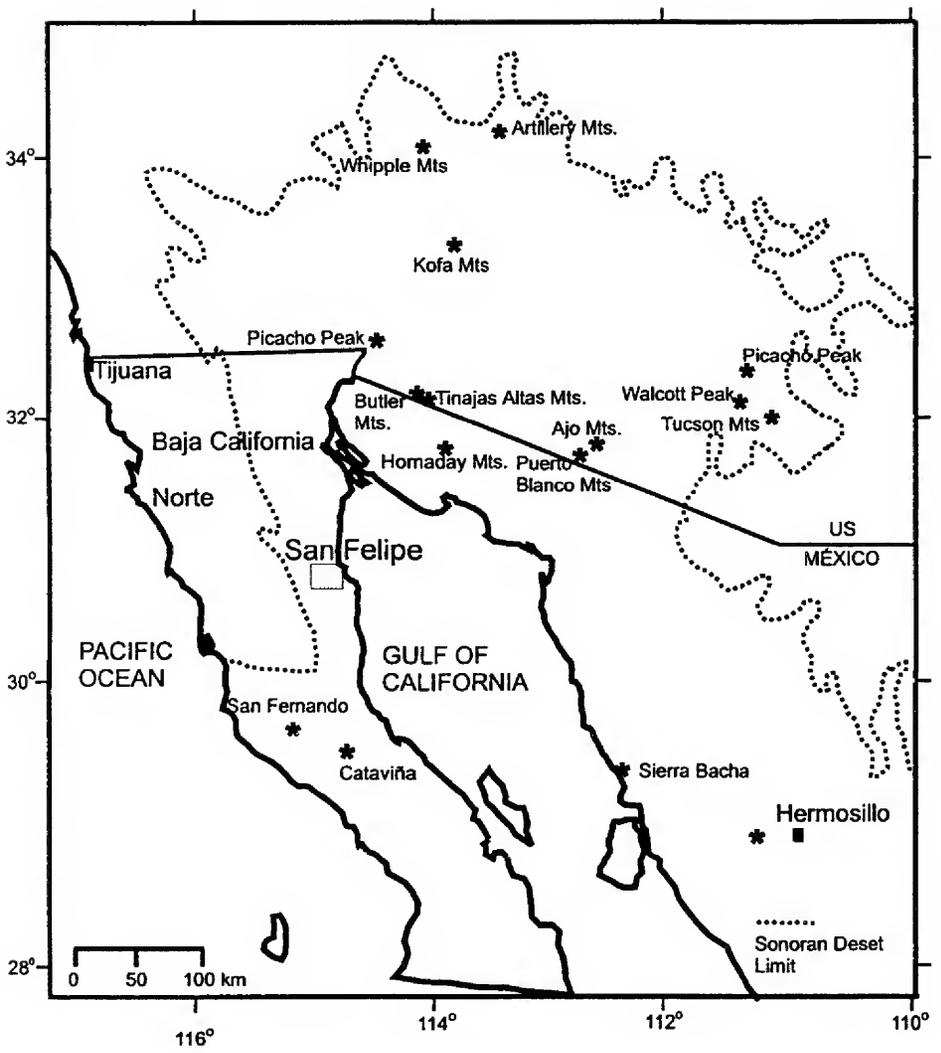


Figure 4.40. Location of the San Felipe site, northern Baja California. * = packrat midden sites. Reprinted from Lozano-García et al. (2002), with permission of Elsevier Science Publishers, Amsterdam.

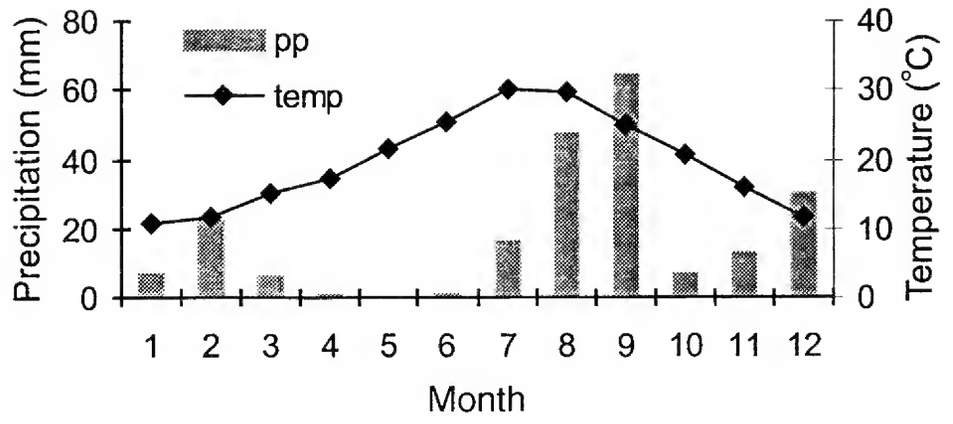


Figure 4.41. Climatogram for Santa Clara weather station near the San Felipe site, 540 m above sea level. Reprinted from Lozano-García et al. (2002), with permission of Elsevier Science Publishers, Amsterdam.

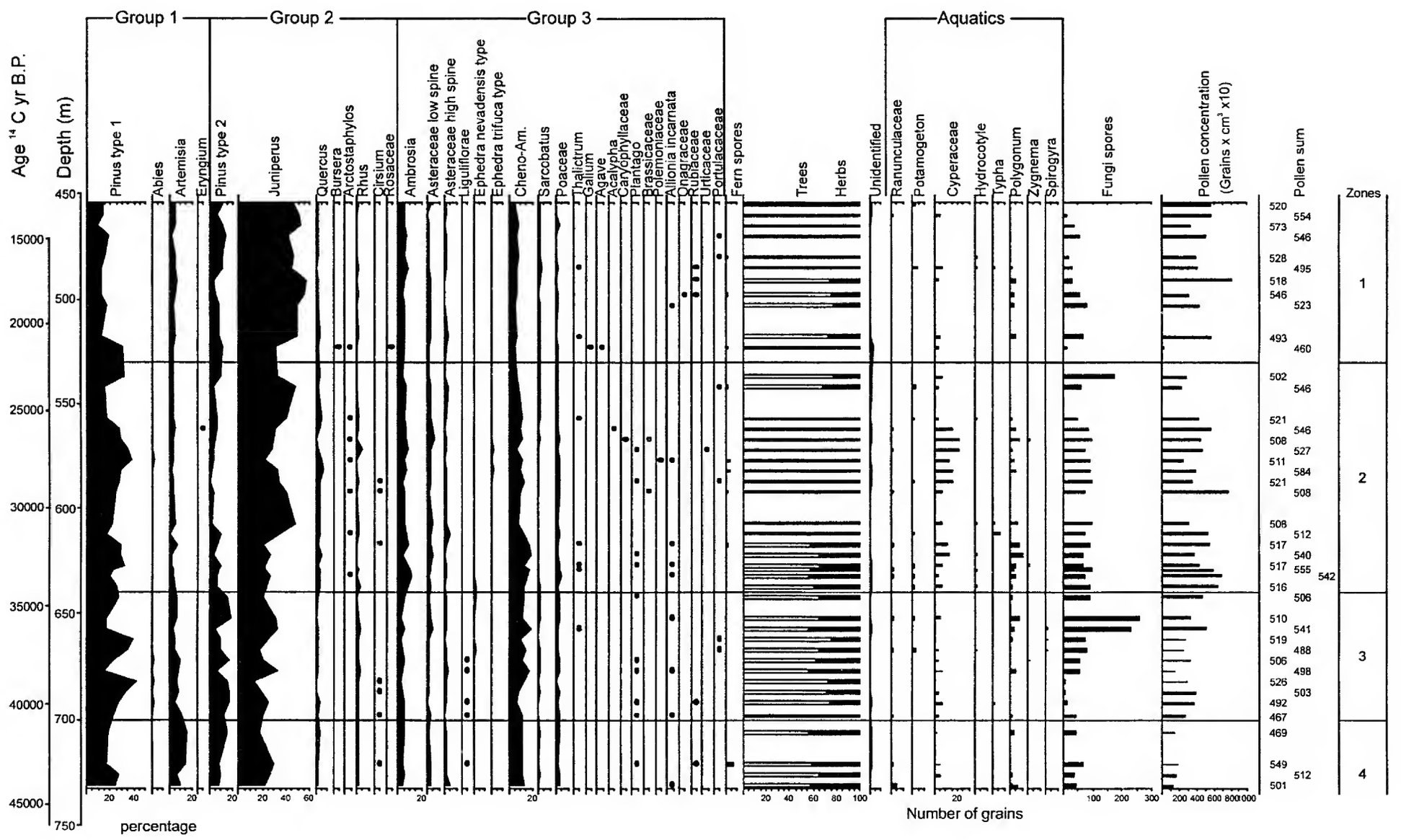


Figure 4.42. Pollen diagram for the San Felipe site. • = pollen 1% or less. Reprinted from Lozano-García et al. (2002), with permission of Elsevier Science Publishers, Amsterdam.

Kyr B.P.), and it is slow at present. The dates are approximate and the annual resolution has been questioned (Betancourt et al., 2002), but the fluctuations in moisture are real. An innovative study involving mites preserved in stalagmites from New Mexico also shows cool-wet phases (~3200–800 years B.P.) in the Holocene (Polyak et al., 2001). Van Devender et al. (1990) conclude, "The variability in community composition through the Holocene was similar in magnitude to the modern variability among different midden sites and appears to reflect the highly variable climate." Considering that shifts toward pluvial climates in the north probably occurred during each of the 18–20 glacial cycles of the past ~2 Ma, with warmer, drier, and more seasonal conditions returning in each of the interglacials, the desert formation is revealed as a dynamic assemblage that has fluctuated in range, composition, and evolutionary impetus throughout the Quaternary.

The potential value of integrating data on modern and fossil vegetation, speciation, and eventually ecosystem history is illustrated by a study of *Larrea tridentata* in arid North America. Diploid, tetraploid, and hexaploid races are aligned across the Chihuahuan, Sonoran, and Mojave deserts. The level of polyploidy is reflected in the size of guard cells in the leaves of modern populations, and in fossil leaves from packrat middens (Hunter et al., 2001). An intricate pattern of migration can be traced across arid North America during the Late Glacial–Holocene, with diploids present in the lower Rio Grande of west Texas and sympatric diploid-tetraploid populations in the lower Colorado Basin of southern California–Arizona 26–10 ^{14}C Kyr B.P.; tetraploids expand from the lower Colorado River Basin into the northern Sonoran Desert by 6.4 ^{14}C Kyr B.P.; and hexaploids are the most recent to appear and reach their current northernmost limit in the Mojave Desert between 5.6 and 3.9 ^{14}C Kyr B.P. As such efforts to integrate neobotany, paleobotany, geology, and climatology become the norm, studies of the Earth's biota approach the ecosystem level as defined in this text.

Figure 4.43. *Quercus rugosa* from the Pleistocene Cerro de La Estrella flora, Iztapalapa, D.F. From Espinosa de G. Rul and Rzedowski (1966). Used with permission of J. Rzedowski.

BASINS OF THE TRANSVOLCANIC BELT AND VICINITY

> "Central Mexico has the largest number of sites and the widest range of palaeoclimatic data in Mexico. The results are, however, difficult to bring together to produce a clear picture." (Metcalfe et al., 2000)

Virtually all information on the Quaternary vegetation of central Mexico comes from plant microfossils (spores, pollen, diatoms). There is a small leaf flora from the Cerro de La Estrella in the Distrito Federal near the village of Iztapalapa east of Mexico City (Espinosa de G. Rul & Rzedowski, 1966). The age is estimated at ~12 Kyr B.P. (Late Glacial), and the flora consists mostly of *Quercus rugosa* (60%; Fig. 4.43), together with *Arbutus*, *Buddleja*, *Ribes*, *Salvia*, *Senecio*, and *Symphoricarpos* (Table 4.1). These are all present in the local vegetation and they occur together where MAP is 850–1150 mm. The site currently receives 600–650 mm, suggesting greater humidity at ~12 Kyr B.P., and this is consistent with recent evidence from plant microfossils.

The first studies to bring attention to the wealth of information available from spore and pollen analysis on the Quaternary of Mexico were those of Paul Sears and Kathryn Clisby (Sears, 1951, 1952, 1955; Clisby & Sears, 1955; Sears & Clisby, 1955; Foreman, 1955) on lacustrine sediments from Lake Texcoco in the Valley of Mexico, and an earlier preliminary investigation on Lake Pátzcuaro in Michoacán by Deevey (1944). Samples were collected from sites in the basin, and from cores previously drilled to test the foundation for the skyscraper Torre Latinoamericana (El Torre) and to study the settling of existing buildings, such as the Palacio de Bellas Artes, as groundwater is drawn from former Lake Texcoco, on which Mexico City is built (Chapter 1). An 80-meter core (Bellas Artes) came from near the Palacio de Bellas Artes, and a 57-meter core (Madero) came from ~250 m to the southeast in the vicinity of the Alameda, a park in the center of Mexico City. These are still the longest cores from the Basin of Mexico.

The techniques can be used to illustrate the methods of the day and the advances made in Quaternary spore and pollen analysis since its early applications. The method for tabulating microfossils was a simple percentage count of 100 tree pollen from each level, without reference to differential preservation

and the considerable difference in pollen transport and production among key components such as *Pinus* and *Quercus*. The problem with percentage counts is that an increase in one component (e.g., *Pinus*, then considered a standard indicator of warm-dry conditions) automatically results in a decrease in the percentages of all others (e.g., *Abies*, *Alnus*, *Quercus*) even if the amounts of the latter remain the same or increase but at a slower rate. The impression is given that a reciprocal relationship exists between the ecological indicators; that is, as *Pinus* increases, *Quercus* appears to decrease, reinforcing the impression that climates are becoming warmer and drier. Also, the amount of pollen through a section varies with rates of sedimentation and with compaction. In sections where there is comparatively little compaction or where sedimentation is rapid, spore and pollen concentration is low. This gives the misimpression that vegetation cover is sparse due to cold or arid climates or that the site had been disturbed through volcanism or human activity. Variable pollen concentration is addressed by calculating the pollen influx (number of grains/equal volumes of sediment throughout the profile). Equal volumes are established for each level by weighing or by introducing an exotic pollen (e.g., *Eucalyptus*) or spores of a typically minor element (*Lycopodium*), then counting fossil grains until a set number of the added forms (e.g., 100) are encountered for each sample. When a number of ^{14}C dates are available, it is also possible to calculate absolute pollen frequency (number of grains/volume of sediment/unit of time). Numerous other tabulating techniques, statistical tests, and innovative ways of presenting the results have improved the reconstruction of vegetation from spore and pollen assemblages. These include calculating percentages of NAP versus AP to reveal periods of open (herbaceous; cold, arid, or disturbed) versus dense (forested; mesic) vegetation. Isopols (lines of equal pollen percentages for a taxon at specific points in time from different sites) reveal directions of movement and, when combined with ^{14}C dates, indicate the time and rates of migration. There are accessory diagrams (fungal spores, seeds, diatoms) and improved dating by magnetostratigraphy, biostratigraphy, tephrochronology (sequence of relative or absolute-dated volcanic ash layers; Newton et al., 2005), and seismic stratigraphy (I: pp. x, 98, 281–282). No radiocarbon dates were available for the Bellas Artes and Madero cores or pollen rain studies to better reconstruct the past vegetation from the diagrams. There was an unawareness of the role of tectonics in altering drainage patterns in basin environments and of the role of ash falls in changing vegetation independent of climate. The early innovative and pioneering works are now mostly of historical interest, and new methodologies are better reflecting the complex Quaternary history of vegetation. Pollen rain studies are now available from several sites in Mexico (Meyer, 1973; Palacios-Chávez, 1977; Jacobs, 1982; Tejero-Diez et al., 1988; Palacios-Chávez & Rzedowski, 1993, pp. 19–24; Orvis, 1998). In the Transvolcanic Belt and vicinity, these studies have confirmed that pollen of *Pinus*, and to a lesser extent *Quercus* and *Alnus*, are all over-represented in pollen diagrams. Under these conditions, diatoms are especially valuable in anchoring the lacustrine phase of the environment by revealing changes in lake levels. Tephra (ash) input affects terrestrial vegetation but has little long-term impact on the diatom flora whose history is determined primarily by climate (Telford et al., 2004).

Closed intermontane basins offer some advantages for studies of vegetation history: (1) they allow the accumulation of long sedimentary records; (2) the modern vegetation and vegetation patterns are relatively simple; (3) pollen of the prominent trees is usually distinctive at the generic level; (4) the closed setting and the relatively recent age of the sediments mean the fossil spores and pollen were probably produced by plants still represented in the vicinity, allowing "probable," cf., or type identifications for some species of stenopalynolous groups; and (5) the zonal belts of vegetation respond quickly to environmental changes that are readily evident from the diagrams.

Closed basins in tectonically active regions, however, are frustratingly difficult places to study vegetation and environmental history based on paleobiological evidence. Lozano-García and Xelhuantzi-López (1997) discuss some of the problems in interpreting Quaternary spore and pollen records from the transvolcanic basins of Mexico. In addition to the relatively few pollen types that dominate the spore and pollen diagrams, there is erosion by wind or water that can remove parts of the section; volcanism (ash and lava) that sets the successional clock back to barren ground and produces seral stages in the recovery vegetation; and fire associated with volcanism that favors the growth of *Pinus* and grasses. Tectonic activity is a special nuisance because it changes drainage and lake levels, thus altering vegetation independent of climate (Chapter 2, Mexico, Transvolcanic Belt; Israde-Alcantara et al., 2005, Lake Pátzcuaro Basin). Not enough adequately dated sections and high-resolution diagrams are available, and there has been long and intense human disturbance of the vegetation. Tools have been found in the Basin of Mexico thought to date from 21,700 ± 320 years B.P. and 24,040 ± 320 years B.P. (fide Garcia-Barcena, 1986). New records of *Zea* (corn) pollen from the Gulf of Tabasco, near the mouth of the Grijalva River, at 5100 calendar years B.C. (6200 ^{14}C years B.P.; Pope et al., 2001) augment 5200-year-old cob remains from the highlands of Oaxaca (Table 4.3). Also recovered from the Grijalva site were pollen of *Manihot* (4600–5800 years B.P.), and seeds of sunflower and pollen of cotton (2500–4000 years B.P.). *Zea* pollen is present at ~4100 years B.P. in the Laguna Catarina watershed just north of Veracruz (Sluyter, 1997). The modern vegetation has been altered for so long in Mexico that results from pollen rain studies are often only marginally applicable to the paleovegetation. These challenges emphasize the need for multidisciplinary projects that employ an array of techniques and allow comparison with well-dated sections across the several basins. These efforts are under way (see the cited studies by Lozano-García and colleagues in the next section), and are reviewed by Metcalfe et al. (2000). Representative studies and the relevant literature are given below, and the localities are shown on Fig. 4.2.

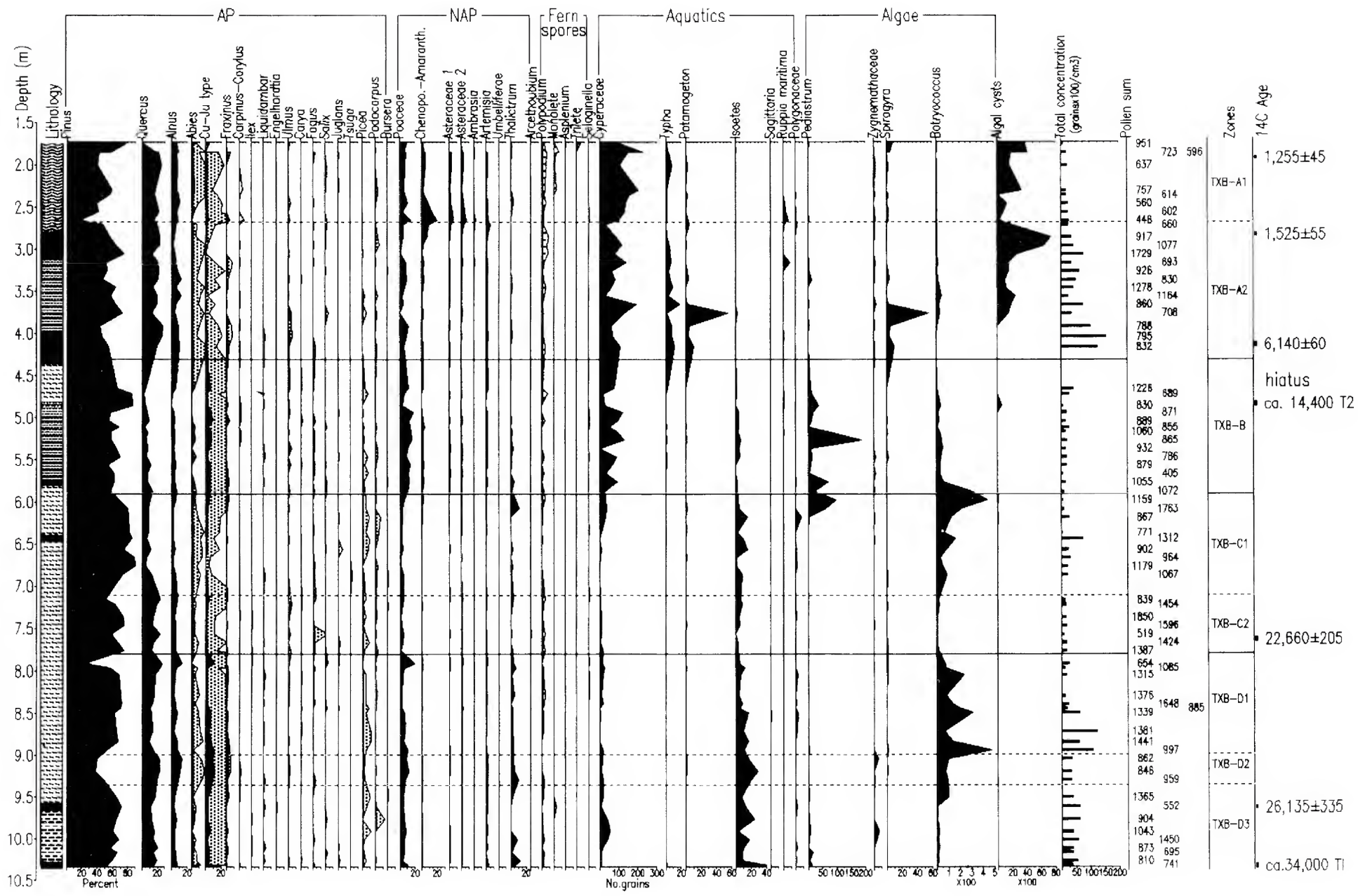


Figure 4.44. Pollen diagram from Lake Texcoco, Basin of Mexico. Reprinted from Lozano-García and Ortega-Guerrero (1998), with permission of Elsevier Science Publishers, Amsterdam.

BASIN OF MEXICO (STATE OF MÉXICO AND THE DISTRITO FEDERAL)

Lake Texcoco—González Quintero and Fuentes Mata, 1980; Lozano-García and Ortega-Guerrero, 1998 (basal date >34 Kyr B.P.)

Tlapacoya (Lake Chalco)—González Quintero, 1986 (33 Kyr B.P.)

Chalco subbasin—Lozano-García et al., 1993; Lozano-García and Ortega-Guerrero, 1994 (20.6 Kyr B.P.); Caballero Miranda, 1997

Laguna de Quila—Almeida-Leñero et al., 1990 (2500–3000 years B.P.)

Agua El Marrano Valley (Ixtaccíhuatl Volcano)—Lozano-García and Vázquez-Selem, 2005

Lake Tecocomulco (northeastern drier part of the Basin of Mexico)—Caballero Miranda et al., 1999

Lakes Zempoala (6320 years B.P.) and Quila (11,610 years B.P.), state of México (Almeida-Leñero et al., 2005)

Lerma Basin (Lake Chignahuapan)—Lozano-García et al., 2005; (Lake Almoloya)—Ludlow-Wiechers et al., 2005

States of Puebla–Tlaxcala region—Ohngemach, 1973; Straka and Ohngemach, 1989 (35 Kyr B.P.)

Tlaloc Crater on La Malinche—Ohngemach, 1977; Straka and Ohngemach, 1989

Zacapú Basin (Michoacán)—Xelhuantzi Lopez, 1994a, b; Metcalfe, 1995; Arnauld et al., 1997 (6090 years B.P.; Ortega et al., 2002)

Lake Cuitzeo (Michoacán)—Israde Alcantara, 1997

Lake Pátzcuaro (Michoacán)—Watts and Bradbury, 1982; Chacón-Torres and Múzquiz-Iribe, 1997 (modern instrumentation record); Bradbury, 2000 (44 Kyr B.P); Metcalfe et al., 2007 (23,000 calendar years, 19,000 ^{14}C years B.P.)

Hoya San Nicolas de Parangueo (Guanajuato)—Brown, 1984, 1985; Metcalfe et al., 1989 (10.7 Kyr B.P.)

In addition to the presence of *Pinus*, *Alnus*, and *Quercus* throughout the sections, there are lesser amounts of *Carya*, *Engelhardia* (*Alfaroa–Oreomunnea*), *Fagus*, *Ilex*, *Liquidambar*, and *Ulmus* (mesic indicators); Cyperaceae, *Ruppia maritima* (alkaline waters), *Thalictrum*, and *Typha* (wet or marsh habitats); and *Isoetes*, *Potamogeton*, and the algae *Botryococcus*, *Pediastrum*, *Spirogyra*, and Zygnemataceae (freshwater aquatics). The assumption that *Pinus* is uniformly an indicator of warm and dry conditions, as in the older literature, is too simplistic for the mountainous regions of central Mexico. Some species (e.g., *Pinus montezumae*, *P. rudis*) are associated with *Abies religiosa* in the cold high-altitude coniferous forest; others (*P. patula*, *P. teocote*) occur with *Quercus* to form the warmer mid-altitude pine-oak forest, and

Table 4.4. Late Glacial and Holocene vegetation changes and climate inferences for Lake Texcoco, Basin of Mexico, fide Lozano-García and Ortega-Guerrero (1998).

Zones/subzones/dates	Vegetation/percentages	Inferred climate
Zone A (Late Glacial [14,400 years B.P.]; middle to late Holocene [6140, 1525, 1255 years B.P.])		cold ~23–10 Kyr B.P.
A1	*Pinus* (low, 36%; higher, 40%–57%; highest, top, 73%), Cyperaceae/ *Typha* marsh	moist
A2	*Pinus* (43%–73%), *Quercus* (increases, 25%–27%), aquatic/marsh taxa	moist
Zone B (no dates; ~14,000–18,000 years B.P.; Late to Middle Glacial)	*Pinus* (43%–73%), high Gramineae (4%–20%), NAP increases, aquatic/marsh increases	dry; moist local habitats
Zone C (18,000–22,800 years B.P.; glacial maximum)		
C1	*Pinus* (90%); *Abies*, *Picea*, *Podocarpus* increase	dry
C2	*Pinus* (50%–80%), *Quercus* (10%–30%), *Alnus* (<3%)	
Zone D (22,600, 26,135, >34,000 years B.P.; Early to Middle Glacial)		cold, dry
(boundary zone)	*Pinus* decreases to 20%; Gramineae increases	
D1	*Pinus* increases (70%–80%), *Quercus* (5%–10%), *Alnus* (<5%)	
D2	*Pinus* decreases (40%–50%), *Quercus* increases (20%–30%), *Alnus* (10%–20%)	cooler than at present, humidity increases
D3	*Pinus* (60%–70%), *Quercus* (10%–20%), *Alnus* (5%–10%); some mesic taxa; *Thalictrum* (5%–30%; moist); aquatics (*Botryococcus*, *Pediastrum*, Zygnemataceae; *Isoetes*)	moist

the pollen of the two groups of *Pinus* cannot be distinguished. The patterns are complex and the climatic implications are not always clear.

The investigations of Lozano-García and Ortega-Guerrero (1998) are used here as an example of the vegetation and climate sequence in the Basin of Mexico, and the results are shown in Fig. 4.44 and in Table 4.4. Four zones with subzones are recognized: >34 Kyr B.P. to 22,600 years B.P., glacial, abundant *Pinus*, becoming cold and dry; 22,800 years B.P. to 18 Kyr B.P., glacial maximum, cold and dry; 14 to 18 Kyr B.P., Late Glacial, more moist; 14,400 to 1255 years B.P., Late Glacial to Holocene, cool-moist. Lachniet and Vázquez-Selem (2005) estimate that at the LGM (21,000–18,000 ^{14}C years B.P.) the ELA (Benn et al., 2005; Harrison, 2005; Mark et al., 2005; see also Electronic Addresses) for central Mexico was at 3400–3950 m. Across the principal volcanoes of central Mexico (among 13 that were glaciated at the LGM), the ELA was lower by ~1000–1500 m. The sequences and the chronology are not apparent in all the basins of the Transvolcanic Belt, and studies of volcanism in the region have proved valuable in explaining some of the perplexing features of the pollen diagram. For example, a decrease in *Pinus* pollen from 80% to 20% at ~22 Kyr B.P. corresponds to an eruption of Popocatépetl between 23,600 and 22,000 years B.P. (Siebe et al., 1995, 1996, 1999; see also Martin del Pozzo et al., 1997). This likely altered the hydrological system as well and accounts for the change in *Pinus* pollen percentages by factors other than climate. There was another eruption at 14 Kyr B.P. (Siebe et al., 1999), and this event correlates with a drop in *Pinus* pollen to a low of 43%.

Lake Chignahuapan is located in the upper valley of the Río Lerma, state of México (Lozano-García et al., 2005). It preserves a 23,000-^{14}C year history of vegetation in a high-altitude setting (2570 m):

- 23,000–11,600 ^{14}C years B.P.—woodland and grassland (open forest). 21,000–16,000 and 12,600 ^{14}C years B.P.—non-arboreal pollen, mostly grasses, correlated with glacial advances MII-1 (24,000–17,000 ^{14}C years B.P.) and MII-2 (17,000–11,600 ^{14}C years B.P.). 19,000–16,000 ^{14}C years B.P.—lower lake level, ELA lower by 930–730 m, temperature lowering of 5°–9° C, timberline lower by 700–900 m. 11,600 ^{14}C years B.P.—Upper Toluca Pumice.
- 10,000 ^{14}C years B.P.—increase in tree pollen, lake level variable.
- 8500 ^{14}C years B.P.—Tres Cruces Tephra.
- 3100 ^{14}C years B.P.—deforestation associated with human activity (Formative Period, 1500 B.C.).
- 1200 ^{14}C years B.P. (550 A.D.)—pollen of *Zea mays* and abundant charcoal.

The increase in coniferous and mixed forests resulting from temperature increases between the late Pleistocene and the Holocene is also recorded at Lake Chalco in the Basin of Mexico.

An indication of the improving nature of late Quaternary climate reconstructions, vegetation histories, and glacial chronologies for central Mexico is noted by Vázquez-Selem (1997, pp. 71–72; Tables 4.5, 4.6). Early results of spore and pollen studies in the Puebla–Tlaxcala Basin (Ohngemach & Straka, 1983) were interpreted to indicate a cool dry climate between 31 and 18 Kyr B.P., but plant microfossils (González-Quintero,

1986) and diatoms (Bradbury, 1989) from the Basin of Mexico now suggest a warm and wet interval between 30 and 24 Kyr B.P. A cool moist period until 8500 years B.P. was earlier proposed for the Puebla–Tlaxcala Basin (Heine & Ohngemach, 1976; Ohngemach & Straka, 1983), while Bradbury (1989) and Metcalfe et al. (1991) show that between 10 and 7 Kyr B.P., it was dry in the Basin of Mexico and in the Lerma Basin. This brings the climate and vegetation sequences more in line with other basins and with regional trends. The landscape was devoid of vegetation following glaciation, and subsequently occupied by alpine grassland between ~10,000 and 7200 years B.P., then by coniferous forest until 6500 years B.P. The mid-Holocene dry period is shown by a return of grassland between 6500 and 5000 years B.P., followed by modern conditions (timberline at ~4000 m) until the present.

Studies including diatom, spore-pollen, and hydrological data have been published for Lake Pátzcuaro on the southern edge of the Mexican Plateau in Michoacán (Watts & Bradbury, 1982; Chacón-Torres & Múzquiz-Iribe, 1997; Bradbury, 2000). Although *Pinus*, *Alnus*, and *Quercus* are predominant throughout the profile, there are changes in other components. At 28–25 Kyr B.P. there is a period of increased moisture (34–21 Kyr B.P. in the Zacapú Basin; Ortega et al., 2002), and freshwater was the deepest and most extensive in Late Glacial and early Holocene time. The likely cause for the increased moisture was a shift of the westerly storm tracks deflected southward by the mile-high Laurentide ice sheet (I: pp. 275–278, 292). This is consistent with the pluvial climates that prevailed in the presently dry regions of northern Mexico. To the west in Nayarit, a record of pollen back to ~6110 years B.P. (Brown, 1985; Brown & Jacobs, 1988) indicates a dry period at ~5000 years B.P. that is part of a subhumid interval widely evident in the basins across central Mexico. Pollen of *Zea* (maize) appears at 3500 years B.P., dating the presence of agriculturalists in the Lake Pátzcuaro Basin.

Collectively, these results indicate that efforts at combining pollen, diatom, glacial, and volcanic proxies with archeological records are beginning to yield a better, although still unsettled, reconstruction of vegetation and paleoenvironments in the transvolcanic basins of Mexico (Metcalfe, 1997; Caballero Miranda et al., 2001; Lozano-García et al., 2005).

Pending

The profile of *Pinus* pollen from Lake Texcoco is reminiscent of that from Lake Tulane, Florida (I: figs. 8.8, 8.9) where the interval between 35,000 and 15,000 years B.P. includes several increases correlated with Heinrich events H 1–4. Sampling at Lake Tulane was at 10 cm, and 20 ^{14}C dates provided high resolution. It is interesting to contemplate whether close sampling and fine dating of material from the Transvolcanic Belt and vicinity, and from the northern desert basins at levels representing the period between 35,000 and 15,000 years B.P., will reveal similar evidence for Heinrich events. Milankovitch and D–O cycles are evident in basin sediments in the Mojave Desert, the Great Basin of western interior United States (Tchakerin & Lancaster, 2002), and possibly in subtropical Brazil (27°S, 49°W; Chapter 7, Quaternary).

There is an extensive literature on the Younger Dryas cold event in Latin America (see *Quaternary Science Reviews*, Vol. 14, 1995). In Mexico, evidence was sought in moraine sequences from the Transvolcanic Belt, and, according to Heine (1994), it was not found. Hansen (1995) views the evidence from Ecuador and Peru as equivocal. However, there are two difficulties in detecting and correlating such events across distant regions. One is that glacial advances depend on both cold temperatures and an adequate supply of moisture for increasing the ice, and the two can vary with local conditions. Another is some uncertainty in dating methods, especially from deposits in carbonate-charged waters, and further confused for the general reader by dates cited as calendar, ^{14}C calibrated, and ^{14}C uncalibrated years. Orvis and Horn (2000) provide a useful recalibration of ^{14}C published to calendar years for convenience of comparison.

Evidence for a Younger Dryas event in Mexico has been found at the following localities:

Northern Mexico (Metcalfe et al., 1997)

Gulf of Mexico (Flower & Kennett, 1990), Gulf of California (Sancetta, 1995; Barron et al., 2004)—deep sea cores

Basin of Mexico (Caballero Miranda, 1995)

Central Mexico (recalibration Malinche volcano M-III advance [Heine, 1978] >10,110–8410 years B.P. [8240 ± 300 ^{14}C years B.P.])

The terrestrial vegetation reflects a Younger Dryas cooling event at the latitudes of southern Mexico (~12,800–11,500 years B.P.), and it was likely a significant forcing mechanism in other parts of Latin America, although not universally expressed at all localities (Chapters 5–7).

In the Zacapú Basin there is a dry period from ~6800–4900 years B.P., and this corresponds in time to the PGCO (7000–5000 years B.P.). Historical records indicate that severe and prolonged droughts prevailed in the Basin of Mexico between 1640 and 1915 A.D. (O'Hara & Metcalfe, 1997). This is partially within the interval of the Little Ice Age, and additional evidence is accumulating that this event was probably expressed in the mid- to low latitudes through reduced precipitation. Vázquez-Selem (1997) has summarized the late Quaternary glacial sequences in central Mexico, including the chronologies of White (1962, 1987) and Heine (1975, 1976, 1988; Table 4.4, with the corresponding climates suggested by Heine). There were three glacial advances at >14,500 years B.P., 14,500–4800 years B.P., and <4800 years B.P. Within the latter there is an advance on Nevado de Toluca at the time of the Little Ice Age. The Jamapa Glacier also formed on the Pico de Orizaba at this time (Palacios et al., 1999), so the Little Ice Age is emerging as another event apparent in the climatic history of Mexico. If so, it is possible that D–O events affected the vegetation and ultimately may be detected in spore and pollen assemblages.

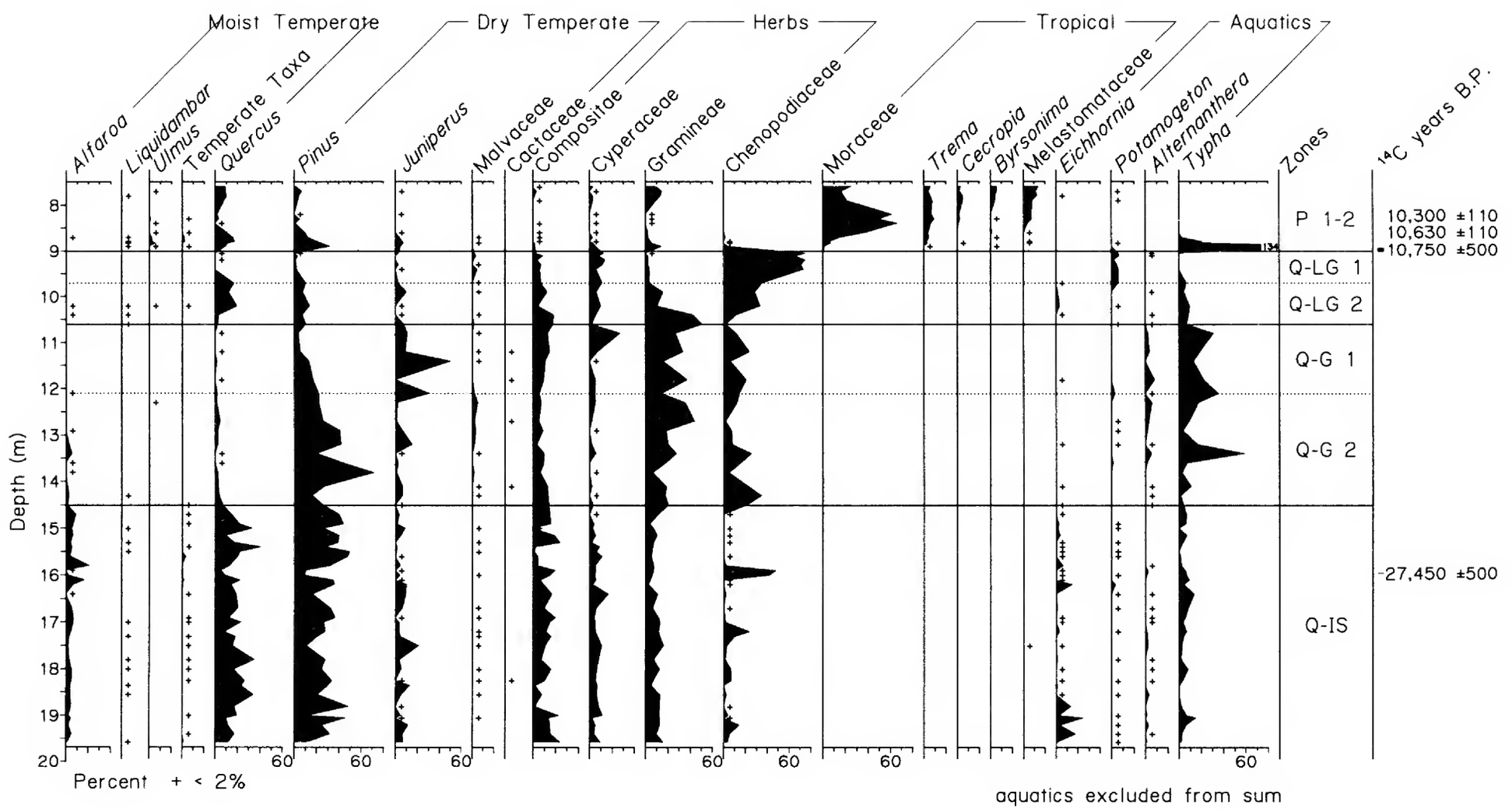


Figure 4.45. Pollen diagram from the Yucatán Peninsula. Reprinted from Leyden et al. (1994), with permission of Elsevier Science Publishers, Amsterdam.

THE ISTHMUS OF TEHUANTEPEC

Two cores were taken along the Middle American Trench near Tehuantepec by the research vessel *Vema* (October 1962), and ^{14}C dates of 8–9 Kyr B.P. were obtained for the basal sediments. The principal pollen identified was *Pinus*, *Alnus*, *Quercus*, and Poaceae–Cyperaceae with smaller amounts of *Abies*, *Liquidambar*, and *Rhizophora* (Habib et al., 1970). The four pollen zones recognized were I (1750 ^{14}C years B.P., moist to dry in the last 1000 years), II (3300 ^{14}C years B.P., dry), III (4050 ^{14}C years B.P., warm, moist), and IV (to an extrapolated 8000–9000 ^{14}C years B.P., dry). Although there were clear fluctuations in climate, these were muted and interpreted to mostly reflect changes in moisture. The zones are based on pollen concentration, as well as composition, on the assumption that high concentration means moist conditions, more dense vegetation, and increased stream flow into the coastal waters. There is no other information available on the vegetation history of the Isthmus of Tehuantepec.

THE YUCATÁN PENINSULA

To the south across the Isthmus of Tehuantepec is the Yucatán Peninsula of Mexico, Belize, and adjacent Guatemala (the Maya region). The lower latitude (~22°–18°N), low, flat topography (average elevation 200 m), and a near-insular setting subdue the effects of temperature fluctuations, and most changes in the vegetation (Fig. 4.45) are related to moisture. The porous limestone karst topography and the flow of water through subsurface channels create dry conditions favoring the growth of shrubland/chaparral–woodland–savanna. This physical control of soil moisture exists even during periods of higher precipitation, including increases in MAP from enhanced hurricane frequency in non-El Niño years, and during globally warm intervals such as in the middle Pliocene and the interglacials. Changes from shrubland to slightly more mesic woodland (increases in *Brosimum*) or toward near-desert, evident in the pollen profiles, likely involve sea level changes that affect water tables. Sea levels were lower by ~120 m during the LGM, and by some proportional amount during each of the previous glacial maxima, and they are expected to rise by ~0.8 m in the coming three to four centuries through the continued melting of glaciers and thermal expansion of ocean waters. These associated fluctuations in water tables (26–40 m lower during glacial maxima) exert a strong influence on the vegetation.

Among the results of pollen, sediment chemistry, and stable isotope records in the Yucatán Peninsula (Leyden et al., 1994, 1996, 1998; Hodell et al., 1995, 2005a; Rosenmeier et al., 2002; see also previous section on The Peopling of Latin America), those of particular interest are (1) evidence for orbital forcing of long-term climate (with imperfectly understood internally controlled shorter-term fluctuations); (2) dry conditions as expected at the LGM (18 Kyr B.P.) when sea levels were lower; (3) an increase in moisture beginning ~9 Kyr B.P.; (4) a period of maximum forest cover at ~7000 and at >4000 years B.P.; (5) the appearance of *Zea mays* at ~4000 years B.P.; and (6) overlap of a particularly dry period between 1785 and 930 years B.P. with the collapse of the Classic Maya civilization (Haug et al., 2003; see also Webster et al., 2007). Between 1400 and 1500 A.D., there is evidence of increased water salinity and a

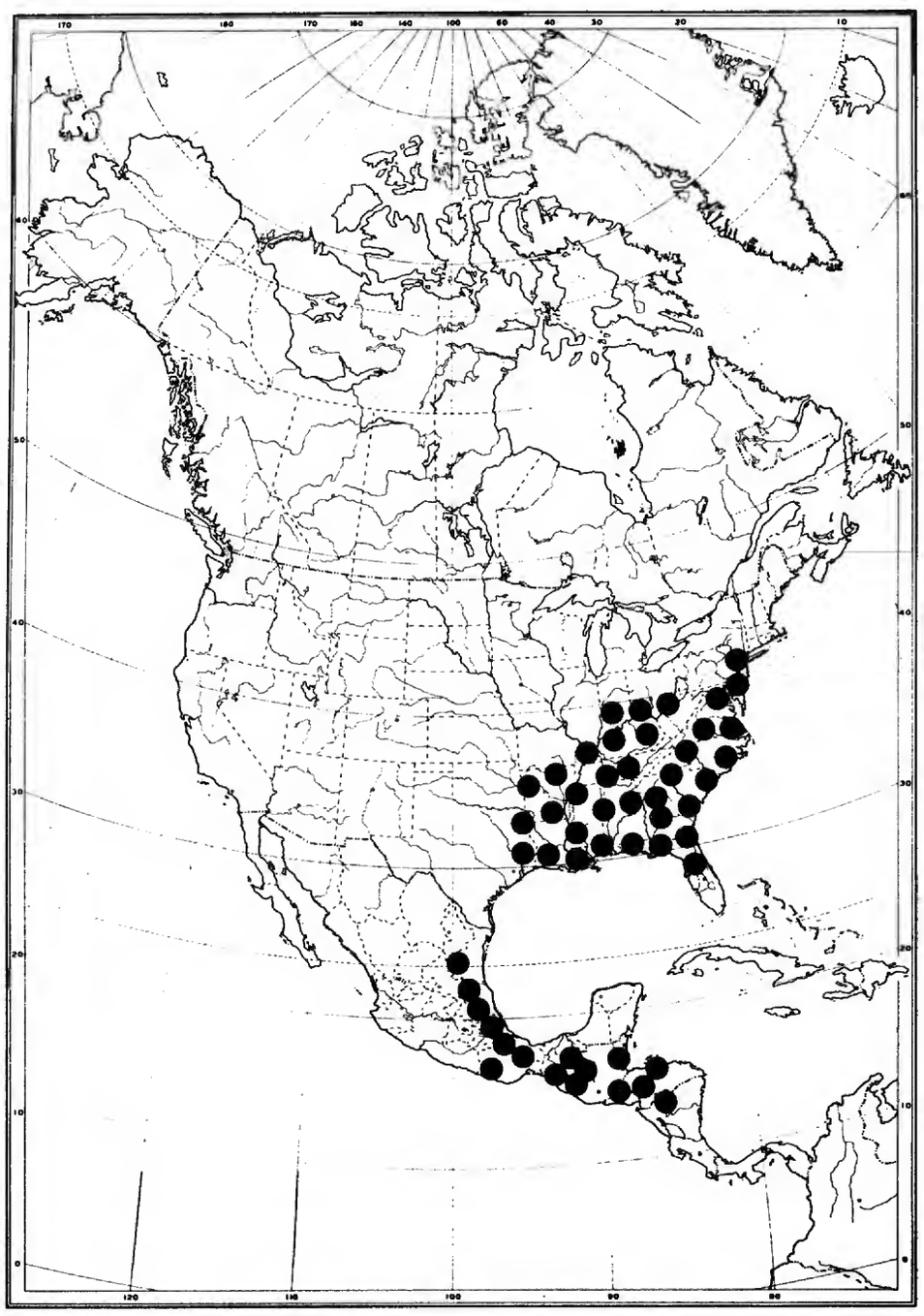


Figure 4.46. Distribution of *Liquidambar styraciflua* in North and Central America. From Rzedowski (1978). Used with permission of Editorial Limusa, México, D.F.

decrease in mesic forests, and there are accounts of cold and famine in Maya and Aztec records corresponding to cool and dry conditions during the Little Ice Age (Hodell et al., 2005b). Although the impact of agriculture on a region is usually reduced vegetation cover, erosion, and aridity, there are instances where dry intervals are circumvented by engineering projects introduced to conserve water. At the Cobá site in the Yucatán Peninsula, there is no evidence of drought at 1000 years B.P., and the probable reason is the construction of dikes that maintained the water level.

AFFINITIES BETWEEN THE MEXICAN–APPALACHIAN VEGETATION

The vegetation of Mexico has been constructed from in situ evolution of native phenotypes and by introductions via long-distance dispersal facilitated by emergence of the Sierra Madre Occidental and Oriental beginning in the Cretaceous, and later by rise of the Transvolcanic Belt, the Chiapas mountains, and the isthmian land bridge. Changes in climate caused migration, and landscape evolution provided a diversity of habitats to accommodate the new lineages and introductions. As a result, the modern Mexican vegetation has affinities with a number of geographic regions, and one of the most prominent is with the deciduous forest of the eastern United States (Figs. 4.46, 4.47; I: pp. 324–327). The floristic relationship is discussed by Fernald (1931), McVaugh (1943), Miranda and Sharp (1950), Sharp (1966), Graham (1966, 1973a, b), and Rzedowski (1978, 1996); the faunal similarities by Martin (1958; Martin & Harrell, 1957); and the molecular/molecular clock aspects of the broader geographic affinities by Hoey and Parks (1991, 1994) and Xiang et al. (1998, 2000). Among the plant genera showing varying degrees of this disjunct distribution are *Pinus*, *Juniperus*, *Taxus*, *Acer*, *Alnus*, *Carpinus*, *Carya*, *Cercis*, *Cornus*, *Epidendrum*, *Fagus*, *Fraxinus*, *Hamamelis*, *Illicium*, *Juglans*, *Liquidambar*, *Magnolia*, *Mitchella*, *Morus*, *Myrica*, *Nyssa*, *Osmanthus*, *Ostrya*, *Platanus*, *Prunus*, *Rhamnus*, *Rhus*, *Smilax*, *Tilia*, and *Ulmus*.

The origin of the relationship was reviewed in Graham (1999b, pp. 324–327) and may be summarized as follows. Early reports by Potzger and Tharp (1943, 1947, 1954) of 11% *Abies* and *Picea* pollen in bogs from central Texas and by Brown (1938) of *Thuja occidentalis* (northern white cedar) in southern Louisiana suggested to Deevey (1949) that the boreal coniferous forest had extended to the Gulf Coast. If so, the deciduous forest would have been displaced even farther

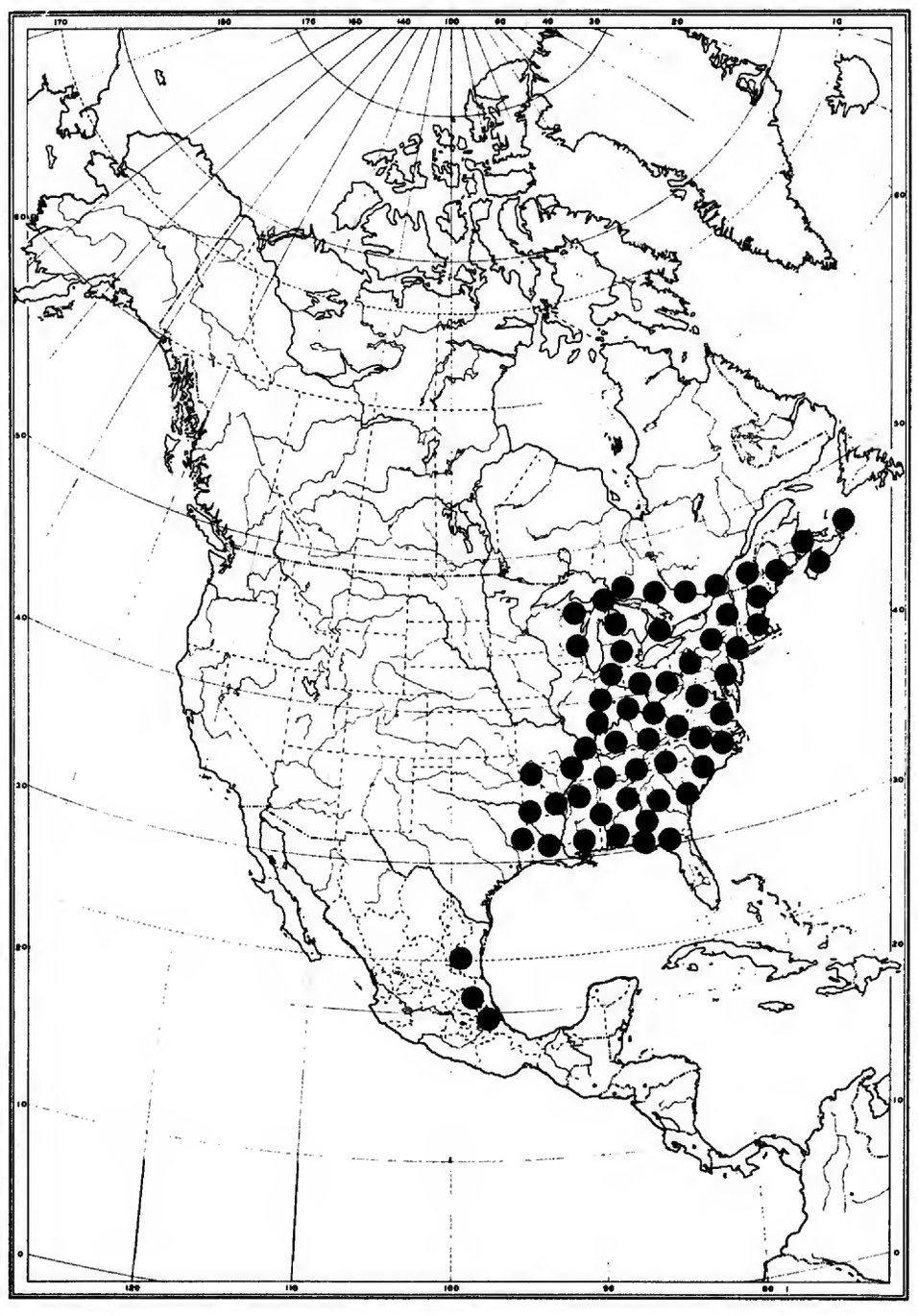


Figure 4.47. Distribution of *Fagus mexicana* in North America. From Rzedowski (1978). Used with permission of Editorial Limusa, México, D.F.

Table 4.5. Correlation of glacial deposits from four sites in central Mexico. From Vázquez-Selem (1997) and references cited therein. See also Metcalfe et al. (2000, p. 709) for comments regarding the White and Heine chronologies.

Teyotl Vázquez-Selem, 1997	**Ixtaccíhuatl-west** White, 1962	**Malinche** Heine, 1975	**Nevado de Toluca** Heine, 1976
T3–rg	Ayoloco recessional	MV–rg	MV–rg
T3	Ayoloco	MIV–rg	MIV–rg
Pumice (4800 years B.P.)			
T2	Milpulco I and II	MII and/or MIII	MIII–3 (?)
Pumice with andesite (~14,500 years B.P.)*	pumiceous lapilli		
T1	Hueyatlaco I and II	?	?

*Also present in lacustrine and peat deposits in the Valley of Mexico and dated by Lozano-García et al. (1993) at ~16,500 years B.P.

Table 4.6. Climates and glacial advances in the highlands of central Mexico for the past 35 Kyr B.P. according to Heine et al. (1975; after Straka & Ohngemach, 1989, p. 120, and references cited therein).

Years B.P.	**Glacier advances**	**Climates (compared to the present)**
100–150	MV	cooler and more humid
		warmer and drier
2000	MIV	somewhat cooler and more humid
		warmer and drier
9000–10,000	MIII	humid and cold
		warmer and drier
12,000	MII	humid and cold
21,000		much colder and drier
		cooler (and drier?)
33,000	MI	humid and cold

south during glacial intervals and isolated in eastern Mexico in interglacial times when the northern deserts were reconstituted. In other words, the origin of the relationship was in the Pleistocene. One of several problems was that some of the plants and animals had differentiated into species pairs (e.g., *Fagus americana–F. mexicana*). This is difficult to reconcile with the implied intermingling of the populations during the 18–20 glacial–interglacial cycles of the past ~2.6 Ma, and with the last ending only ~12 Kyr.

The problem was resolved when a recount showed that the 11% *Abies* and *Picea* pollen was only 1.5% *Picea* alone (three grains in a count of 200) as spruce extended its range southward to within wind-transport distance of the Texas bogs during the LGM and early Holocene (Graham & Heimsch, 1960). Furthermore, Delcourt and Delcourt (1977) found that the megafossils reported as *Thuja occidentalis* were actually *Chamaecyparis thyoides* (southern yellow cedar). This still left open the question of when the northern temperate elements became established in eastern Mexico. It was answered, in part, by the discovery of pollen of *Pinus*, *Alnus*, *Ilex*, *Juglans*, *Liquidambar*, *Myrica*, *Populus*, *Quercus*, *Smilax*, and *Ulmus* in the middle Pliocene Paraje Solo Formation of eastern Mexico (Graham, 1976a, b) and megafossils of *Platanus*, *Populus*, *Quercus*, and *Salix* in the Pliocene of Hidalgo (Aguilar & Velasco de León, 2002). The principal time(s) when various northern temperate elements migrated into Latin America, or persisted and ecologically differentiated there from ancient lineages, or were introduced by long-distance transport, are discussed in Chapter 8. A propitious time would have been in and after the middle Miocene when there was a significant drop in global MATs (Fig. 4.3). At any rate, recent studies indicate it was before the Pleistocene.

NOTES

1. *Trichipteris* is now considered to be an unnatural (polyphyletic) genus better included in an expanded *Cyathea*. Similarly, *Sphaeropteris*, as defined by Tryon, is polyphyletic. The 17 New World species admitted by Tryon are more closely allied to various groups of species within *Cyathea* sensu lato. By recent revisions *Antrophyum* becomes an Old World genus, and *Polytaenium* is adopted for most of the New World species formerly included in *Antrophyum* (Alan Smith, pers. comm., 1999).

2. Monsoon (from the Arabic "mausim," meaning "season")—a wind blowing part of the year from one direction, typically bringing a season of heavy rainfall, and blowing from another direction for the rest of the year. Part of the cause is the great seasonal temperature difference over the affected landmass. The term is traditionally used for winds off the Indian Ocean (southwesterly from May to September), but presently applied to any region with directional winds and a distinct rainy season (see e.g., The Arizona "Monsoon" at http://www.ag.arizona.edu/maricopa/garden/html/weather/monsoon.htm).

REFERENCES

Adams, C. G., D. E. Lee, and B. R. Rosen. 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 77: 289–313.

Aguilar, F. J. and P. Velasco de León. 2002. El clima durante el Plioceno en la región de Santa María Amajac, Hidalgo, Mexico. Bol. Soc. Bot. Mexico 71: 71–81.

Akers, W. H. 1979. Planktic foraminifera and calcareous nannoplankton biostratigraphy of the Neogene of Mexico. Part 1—Middle Pliocene. Tulane Stud. Geol. & Paleontol. 15: 1–32.

Alley, R. B. 2000. The Two-Mile Time Machine: Ice Cores, Abrupt Climate Change, and Our Future. Princeton University Press, Princeton, NJ.

Almeida-Leñero, L. et al. (+ 6 authors). 1990. Paleoecología en el area de La Laguna de Quila, estado de México. Revista Soc. Mex. Paleontol. 2: 93–101.

———, H. Hooghiemstra, A. M. Cleef, and B. van Geel. 2005. Holocene climatic and environmental change from pollen records of lakes Zempoala and Quila, central Mexican highlands. Rev. Palaeobot. Palynol. 136: 63–92.

Anderson, R. S. and T. R. Van Devender. 1995. Vegetation history and paleoclimates of the coastal lowlands of Sonora, Mexico—Pollen records from packrat middens. J. Arid Environm. 30: 295–306.

Arnauld, C., S. E. Metcalfe, and P. Petrequin. 1997. Holocene climatic change in the Zacapú Lake Basin, Michoacán: Synthesis of results. Quatern. Int. 43/44: 173–179.

Axelrod, D. I. 1940. The Mint Canyon flora of southern California: A preliminary statement. Amer. J. Sci. 238: 577–585.

———. 1979. Age and origin of Sonoran Desert vegetation. Occas. Pap. Calif. Acad. Sci. 132: 1–74.

Bains, S., R. D. Norris, R. M. Corfield, and K. L. Faul. 2000. Termination of global warmth at the Paleocene/Eocene boundary through productivity feedback. Nature 407: 171–174.

Barron, J. A., D. Bukry, and J. L. Bischoff. 2004. High resolution paleoceanography of the Guaymas Basin, Gulf of California, during the past 15,000 years. Mar. Micropaleontol. 50: 185–207.

Bartlett, A. S., E. S. Barghoorn, and R. Berger. 1969. Fossil maize from Panama. Science 165: 389–390.

Becerra, J. X. 2005. Timing the origin and expansion of the Mexican tropical dry forest. Proc. Natl. Acad. Sci. U.S.A. 102: 10919–10923.

Benn, D. I. et al. (+ 5 authors). 2005. Reconstruction of equilibrium-line altitudes for tropical and sub-tropical glaciers. Quatern. Int. 138/139: 8–21.

Berry, E. W. 1923. Miocene plants from southern Mexico. Proc. U. S. Natl. Mus. 62: 1–27.

Betancourt, J. L., H. D. Grissino-Mayer, M. W. Salzer, and T. W. Swetnam. 2002. A test of "annual resolution" in stalagmites using tree rings. Quatern. Res. 58: 197–199.

Binford, M. W. et al. (+ 5 authors). 1987. Ecosystems, paleoecology and human disturbance in subtropical and tropical America. Quatern. Sci. Rev. 6: 115–128.

Bintanja, R., R. S. W. van de Wal, and J. Oerlemans. 2005. Modeled atmospheric temperatures and global sea levels over the past million years. Nature 437: 125–128.

Bradbury, J. P. 1989. Late Quaternary lacustrine paleoenvironments in the Cuenca de Mexico. Quatern. Sci. Rev. 8: 75–100.

———. 1997. Sources of glacial moisture in Mesoamericana. Quatern. Int. 43/44: 97–110.

———. 2000. Limnological history of Lago de Pátzcuaro, Michoacán, Mexico for the past 48,000 years: Impacts of climate and man. Palaeogeogr. Palaeoclimatol. Palaeoecol. 163: 69–95.

Bradley, R. S., M. K. Hughes, and H. F. Diaz. 2003. Climate in medieval time. Science 302: 404–405.

Braun, H. et al. (+ 7 authors). 2005. Possible solar origin of the 1,470-year glacial climate cycle demonstrated in a coupled model. Nature 438: 208–211.

Bremer, K. 1994. Asteraceae: Cladistics and Classification. Timber Press, Portland, OR.

Brinkhuis, H. et al. (+ 21 authors and the Expedition 302 Scientists). 2006. Episodic fresh surface waters in the Eocene Arctic Ocean. Nature 441: 606–609.

Broecker, W. S. 2006. Was the Younger Dryas triggered by a flood? Science 312: 1146–1148.

Brook, G. A., B. B. Ellwood, L. B. Railsback, and J. B. Cowart. 2006. A 164 ka record of environmental change in the American Southwest from a Carlsbad Cavern speleothem. Palaeogeogr. Palaeoclimatol. Palaeoecol. 237: 483–507.

Brown, C. A. 1938. The flora of Pleistocene deposits in the western Florida Parishes, west Feliciana Parish, and east Baton Rouge Parish, Louisiana. *In:* H. N. Fisk, H. G. Edwards, C. A. Brown, and W. C. Steere (eds.), Contributions to the Pleistocene History of the Florida Parishes of Louisiana. Louisiana Geological Survey Bulletin 12, New Orleans. pp. 59–96.

Brown, K. 2001. New trips through the back alleys of agriculture. Science 292: 631–633.

Brown, R. B. 1984. The paleoecology of the northern frontier of Mesoamerica. Ph.D. Dissertation, University of Arizona, Tucson.

———. 1985. Summary of late-Quaternary pollen records from Mexico west of the Isthmus of Tehuantepec: *In:* V. M. Bryant and R. G. Holloway (eds.), Pollen Records of Late Quaternary North American Sediments. American Association of Stratigraphic Palynologists, Dallas. pp. 71–93.

——— and B. F. Jacobs. 1988. Análisis e interpretación del polen de dos lagos del occidente de México. Palynológica et Palaeobotánica 1: 45–59.

Burnham, R. and A. Graham. 1999. The history of Neotropical vegetation: New developments and status. Ann. Missouri Bot. Gard. 86: 546–589.

Bush, M. B., D. R. Piperno, and P. A. Colinvaux. 1989. A 6,000 year history of Amazonian maize cultivation. Nature 340: 303–305.

Byrne, R. and S. P. Horn. 1989. Prehistoric agriculture and forest clearance in the Sierra de Los Tuxtlas, Veracruz, Mexico. Palynology 13: 181–193.

Caballero Miranda, M. 1995. Late Quaternary palaeolimnology of Lake Chalco, the Basin of Mexico: New evidence for palaeoenvironmental and palaeoclimatic change in Central Mexico during the last 45,000 years. Ph.D. Dissertation, University of Hull, Hull, U.K.

———. 1997. The last glacial maximum in the Basin of Mexico: The diatom record between 34,000 and 15,000 years B.P. from Lake Chalco. Quatern. Int. 43/44: 125–136.

———, S. Lozano-García, B. Ortega, J. Urruita, and J. L. Macias. 1999. Environmental characteristics of Lake Tecocomulco, northern Basin of Mexico, for the last 50,000 years. J. Paleolimnol. 22: 399–411.

———, J. L. Macías, S. Lozano-García, J. Urrutia-Fucugauchi, and R. Castañeda-Bernal. 2001. Late Pleistocene–Holocene volcanic stratigraphy and paleoenvironments of the upper Lerma Basin, Mexico. Special Publ. Int. Assoc. Sedimentol. 30: 247–261.

Caligari, P. D. S. and D. J. N. Hind. 1996. Compositae: Biology and Utilization. Proceedings of the International Compositae Conference, Vol. 2. Royal Botanic Gardens, Kew, Richmond, U.K.

Cevallos-Ferriz, S. R. S. 1992. Tres maderas de gimnospermas Cretácias del norte de México. Anales Inst. Biol. Univ. Nac. Auton. Mexico, Bot. 63: 111–137.

——— and R. Weber. 1992. Dicotyledonous wood from the Upper Cretaceous (Maastrichtian) of Coahuila. Revista Univ. Nac. Auton. Mexico Inst. Geol. 10: 65–70.

Chacón-Torres, A. and E. Múzquiz-Iribe. 1997. Climatic trends, water balance and Lake Pátzcuaro, a tropical high altitude lake. Quatern. Int. 43/44: 43–51.

Clisby, K. H. and P. B. Sears. 1955. Palynology in southern North America. Part III: Microfossil profiles under Mexico City correlated with the sedimentary profiles. Geol. Soc. Amer. Bull. 66: 511–520.

Cooke, R. G. 1998. Human settlement of Central America and northernmost South America (14,000–8000 B.P.). Quatern. Int. 49/50: 177–190.

Coronato, A., M. Salemme, and J. Rabassa. 1999. Palaeoenvironmental conditions during the early peopling of southernmost South America (Late Glacial–early Holocene, 14–8 ka B.P.). Quatern. Int. 53/54: 77–92.

Cramer, B. S. and D. V. Kent. 2005. Bolide summer: The Paleocene/Eocene thermal maximum as a response to an extraterrestrial trigger. Palaeogeogr. Palaeoclimatol. Palaeoecol. 224: 144–166.

Crepet, W. L. and G. D. Feldman. 1991. The earliest remains of grasses in the fossil record. Amer. J. Bot. 78: 1010–1014.

Cross, A. T., G. G. Thompson, and J. B. Zaitzeff. 1966. Source and distribution of palynomorphs in bottom sediments, southern part of Gulf of California. Mar. Geol. 4: 467–524.

——— and E. Martínez-Hernández. 1980. Compositae pollen in Early Tertiary rocks, Baja California, Mexico. Abstract, 5th International Palynological Conference, Cambridge, U.K.

Curtis, J. H., D. A. Hodell, and M. Brenner. 1996. Climate variability on the Yucatán Peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. Quatern. Res. 46: 37–47.

Deevey, E. S., Jr. 1944. Pollen analysis and Mexican archeology. An attempt to apply the method. Amer. Antiquity 10: 135–149.

———. 1949. Biogeography of the Pleistocene. Geol. Soc. Amer. Bull. 60: 1315–1416.

Delcourt, P. A. and H. R. Delcourt. 1977. The Tunica Hills, Louisiana–Mississippi: Late Glacial locality for spruce and deciduous forest species. Quatern. Res. 7: 218–237.

Dick, C. W. and S. J. Wright. 2005. Tropical mountain cradles of dry forest diversity. Proc. Natl. Acad. Sci. U.S.A. 102: 10757–10758.

Dillehay, T. 1989. Monte Verde: A Late Pleistocene Settlement in Chile. Vol. I: Paleoenvironment and Site Context. Smithsonian Institution Press, Washington, D.C.

———. 1997. Monte Verde: A Late Pleistocene Settlement in Chile. Vol. II: The Archaeological Context and Interpretation. Smithsonian Institution Press, Washington, D.C.

———. 2002. Climate and human migrations. Science 298: 764–765.

Doubinger, J. and P. Chotin. 1975. Étude palynologique de lignites Tertiaires du Bassin d'Arauco–Concepción (Chile). Revista Española Micropaleontol. 7: 549–565.

Eldrett, J. S., I. C. Harding, P. A. Wilson, E. Butler, and A. P. Roberts. 2007. Continental ice in Greenland during the Eocene and Oligocene. Nature 446: 176–179.

Elias, S. A. 1992. Late Quaternary zoogeography of the Chihuahuan Desert insect fauna, based on fossil records from packrat middens. J. Biogeogr. 19: 285–297.

———, T. R. Van Devender, and R. de Baca. 1995. Insect fossil evidence of Late Glacial and Holocene environments in the Bolsón de Mapimí, Chihuahuan Desert, Mexico: Comparisons with the paleobotanical record. Palaios 10: 454–464.

Ellison, C. R. W., M. R. Chapman, and I. R. Hall. 2006. Surface and deep ocean interactions during the cold climate event 8200 years ago. Science 312: 1929–1932.

Espinosa de G. Rul, J. and J. Rzedowski. 1966. Flórula del Pleistoceno superior del Cerro de La Estrella, próximo a Ixtapalapa, D. F. (México). Anales Esc. Nac. Ci. Biol. (Mexico City) 16: 9–39.

Estrada-Ruiz, E. and S. R. S. Cevallos-Ferriz. 2007. Infructescences from the Cerro del Pueblo Formation (late Campanian), Coahuila, and El Cien Formation (Oligocene–Miocene), Baja California Sur, Mexico. Int. J. Pl. Sci. 168: 507–519.

———, H. I. Martínez-Cabrera, and S. R. S. Cevallos-Ferriz. 2007. Fossil woods from the late Campanian–early Maastrichtian Olmos Formation, Coahuila, Mexico. Rev. Palaeobot. Palynol. 145: 123–133.

Felix, J. and A. G. Nathorst. 1893. Versteinerungen aus dem Mexicanischen Staat Oaxaca. *In:* J. Felix and H. Lenk (eds.), Beiträge zur Geologie und Paläontologie der Republik Mexico, Teil 2. Felix, Leipzig. pp. 39–54.

Fernald, M. L. 1931. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora 33: 25–63. [Reprinted as Contrib. Gray Herb. 93.]

Flower, B. P. and J. P. Kennett. 1990. The Younger Dryas cool episode in the Gulf of Mexico. Paleoceanography 5: 949–961.

Folan, W. J. and B. H. Hyde. 1985. Climatic forecasting and recording among the ancient and historic Maya, an ethnohistoric approach to epistemological and paleoclimatological patterning. *In:* W. J. Folan (ed.), Contributions to the Archaeology and Ethnohistory of Greater Mesoamerica. Southern Illinois University Press, Carbondale. pp. 15–48.

Foreman, F. 1955. Palynology in southern North America. Part II: Study of two cores from lake sediments of the Mexico City Basin. Geol. Soc. Amer. Bull. 66: 475–510.

Fournier, G. R. 1982. Palynostratigraphic analysis of cores from site 493, Deep Sea Drilling Project Leg 66. Initial Reports of the Deep Sea Drilling Project 66: 661–670.

Fox, D. L. and P. L. Koch. 2003. Tertiary history of C_4 biomass in the Great Plains, USA. Geology 31: 809–812.

Frost, S. H. and R. L. Langenheim Jr. 1974. Cenozoic Reef Biofacies: Tertiary Larger Foraminifera and Scleractinian Corals from Chiapas, Mexico. Northern Illinois University Press, DeKalb.

Gagan, M. K. et al. (+ 6 authors). 2000. New views of tropical paleoclimates from corals. Quatern. Sci. Rev. 19: 45–64.

Garcia-Barcena, J. 1986. Algunos aspectos chronológicos. *In:* J. L. Lorenzo and L. Mirambell (eds.), Tlapacoya: 35,000 Años de Historia del Lago de Chalco. Colección Científica, Serie Prehistoria. INAH, México, D.F. pp. 219–224.

Gibbons, A. 1997. Monte Verde: Blessed but not confirmed. Science 275: 1256–1257.

Goebel, T., M. R. Waters, and M. Dikova. 2003. The archaeology of Ushki Lake, Kamchatka, and the Pleistocene peopling of the Americas. Science 301: 501–505.

Gómez-Pompa, A. 1973. Ecology of the vegetation of Veracruz. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 73–148.

González, S., D. Huddart, M. R. Bennett, and A. González-Huesca. 2006. Human footprints in central Mexico older than 40,000 years. Quatern. Sci. Rev. 25: 201–222.

González-José, R. et al. (+ 6 authors). 2003. Craniometric evidence for Palaeoamerican survival in Baja California. Nature 425: 62–65.

González Quintero, L. 1986. Análisis polínicos de los sedimentos. *In:* J. L. Lorenzo and L. Mirambell (eds.), Tlapacoya: 35,000 Años de Historia del Lago de Chalco. Colección Cientifica, Serie Prehistoria. Instituto Nacional de Antropología e Historia, México, D.F. pp. 157–166.

——— and L. Fuentes Mata. 1980. El Holoceno de la porción central de la Cuenca de México. *In:* F. Sanchez (ed.), Memorias III Coloquio sobre Paleobotánica y Palinología, Colección Científica, Instituto Nacional de Antropología e Historia, México, D.F. pp. 113–132.

Graham, A. 1966. Plantae Rariores Camschatcenses: A translation of the dissertation of Jonas P. Halenius, 1750. Brittonia 18: 131–139.

———. 1973a. Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam.

———. 1973b. History of the arborescent temperate element in the Latin American biota. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 301–314.

———. 1976a. Studies in Neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63: 787–842.

———. 1976b. Late Cenozoic evolution of tropical lowland vegetation in Veracruz, Mexico. Evolution 29: 723–735.

———. 1980. Morfología del polen de *Eugenia/Myrcia* (Myrtaceae) y *Combretum/Terminalia* (Combretaceae) en relacíon a su alcance stratigráfico en el Terciario de Caribe. Biotica 5: 5–14.

———. 1994. Neotropical Eocene coastal floras and $^{18}O/^{16}O$-estimated warmer vs. cooler equatorial waters. Amer. J. Bot. 81: 301–306.

———. 1995. Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. Biotropica 27: 20–27.

———. 1996. A. contribution to the geologic history of the Compositae. *In:* D. J. N. Hind and H. J. Beentje (eds.), Compositae: Systematics. Proceedings of the International Compositae Conference, Vol. 1. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 123–140.

———. 1999a. Studies in Neotropical paleobotany. XIII. An Oligo–Miocene palynoflora from Simojovel (Chiapas, Mexico). Amer. J. Bot. 86: 17–31.

———. 1999b. Late Cretaceous and Cenozoic History of North American Vegetation (north of Mexico). Oxford University Press, Oxford, U.K.

———. 2000. Palynofloras and terrestrial environments in the Eocene of the Caribbean Basin. GFF (Geologiska Föreningen, Sweden) 122: 64.

———. 2003. The concepts of deep-time floras and paleobotanical hot-spots. Syst. Bot. 28: 461–464.

———. 2006. Paleobotanical evidence and molecular data in reconstructing the historical phytogeography of Rhi-

zophoraceae. *In:* A. Graham (ed.), Biogeography of Latin America—Causes and Effects. Ann. Missouri Bot. Gard. 93: 325–334.

——— and D. L. Dilcher. 1995. The Cenozoic record of tropical dry forest in northern Latin America and the southern United States. *In:* S. H. Bullock, H. A. Mooney, and E. Medina (eds.), Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, U.K. pp. 124–145.

——— and C. Heimsch. 1960. Pollen studies of some Texas peat deposits. Ecology 41: 751–763.

——— and R. Palacios Chávez. 1996. Additions and preliminary study of an Oligo–Miocene palynoflora from Chiapas, Mexico. Rheedea 6: 1–12.

Grosjean, M. and L. Núñez A. 1994. Late Glacial, early and middle Holocene environments, human occupation, and resource use in the Atacama (northern Chile). Geoarchaeology 9: 271–286.

Guthrie, R. D. 2006. New carbon dates link climate change with human colonization and Pleistocene extinctions. Nature 441: 207–209.

Habib, D., D. Thurber, D. Ross, and J. Donahue. 1970. Holocene palynology of the Middle America Trench near Tehuantepec, Mexico. Geol. Soc. Amer. Mem. 126: 233–261.

Hadingham, E. 2004. America's first immigrants. Smithsonian (November): 91–98.

Hansen, B. C. S. 1995. A review of Late Glacial pollen records from Ecuador and Peru with reference to the Younger Dryas Event. Quatern. Sci. Rev. 14: 853–865.

Harrison, S. P. 2005. Editorial—Snowlines at the last glacial maximum and tropical cooling. Quatern. Int. 138/139: 5–7.

Haug, G. H. et al. (+ 5 authors). 2003. Climate and the collapse of Maya civilization. Science 299: 1731–1735.

Heine, K. 1975. Studien zur jüngquatären Glazialmorphologie Mexikanischer Vulkane, mit einen Ausblick auf die Klimageschichte. Das Mexiko–Projekt der Deutschen Forschungsgemeinschaft, Vol. VII. Franz Steiner Verlag, Wiesbaden, Germany.

———. 1976. Blockgletscher—und Blockzungen–Generationen am Nevado de Toluca, Mexiko. Erde (Berlin) 107: 330–352.

———. 1978. Neue Beobachtungen zur Chronostratigraphie der mittelwisconsinzeitlichen Vergletscherungen und Böden Mexikanischer Vulkane. Eiszeitalter & Gegenwart 28: 139–147.

———. 1988. Late Quaternary glacial chronology of the Mexican volcanoes. Geowissenschaften 6 Jahrg., Nr. 7: 197–205.

———. 1994. The Late Glacial moraine sequences in Mexico: Is there evidence for the Younger Dryas event? Palaeogeogr. Palaeoclimatol. Palaeoecol. 112: 113–123.

——— and D. Ohngemach. 1976. Die Pleistozän/Holozän Grenze in Mexiko. Münstersche Forschungen zur Geologie und Paläontologie 38/39: 229–251.

Henderson, G. M. 2006. Caving in to new chronologies. Science 313: 620–622. [Speleothems formed in caves, such as stalagmites, can be dated precisely and are increasingly providing detailed and accurate records of past climates.]

Hernández-Castillo, G. R. and S. R. S. Cevallos-Ferriz. 1999. Reproductive and vegetative organs with affinities to Haloragaceae from the Upper Cretaceous Huepac Chert locality of Sonora, Mexico. Amer. J. Bot. 86: 1717–1734.

Hind, D. J. N. and H. J. Beentje (eds.). 1996. Compositae: Systematics. Proceedings of the International Compositae Conference, Vol. 1. Royal Botanic Gardens, Kew, Richmond, U.K.

Hodell, D. A. et al. (+ 6 authors). 2005a. Climate change on the Yucatán Peninsula during the Little Ice Age. Quatern. Res. 63: 109–121.

———, M. Brenner, and J. H. Curtis. 2005b. Terminal classic drought in the northern Maya lowlands inferred from multiple sediment cores in Lake Chichancanab (Mexico). Quatern. Sci. Rev. 24: 1413–1427.

———, ———, ———, and T. Guilderson. 2001. Solar forcing of drought frequency in the Maya lowlands. Science 292: 1367–1370.

———, J. H. Curtis, and M. Brenner. 1995. Possible role of climate in the collapse of Classic Maya civilization. Nature 375: 391–394.

Hoey, M. T. and C. R. Parks. 1991. Isozyme divergence between eastern Asian, North American, and Turkish species of *Liquidambar* (Hamamelidaceae). Amer. J. Bot. 78: 938–947.

——— and ———. 1994. Genetic divergence in *Liquidambar styraciflua*, *L. formosana*, and *L. acalycina* (Hamamelidaceae). Syst. Bot. 19: 308–316.

Holmgren, C. A., M. C. Peñalba, K. A. Rylander, and J. L. Betancourt. 2003. A 16,000 ^{14}C yr B.P. packrat midden series from the U.S.A.–Mexico borderlands. Quatern. Res. 60: 319–329.

Hunter, K. L. et al. (+ 5 authors). 2001. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. Global Ecol. Biogeogr. 10: 521–533.

Hurst, W. J., S. M. Tarka Jr., T. G. Powis, F. Valdez Jr., and T. R. Hester. 2002. Cacao usage by the earliest Maya civilization. Nature 418: 289–290.

Israde-Alcantara, I. 1997. Neogene diatoms of Cuitzeo Lake, central sector of the Trans-Mexican Volcanic Belt and their relationship with the volcano-tectonic evolution. Quatern. Int. 43/44: 137–143.

———, V. H. Garduño-Monroy, C. T. Fisher, H. P. Pollard, and M. A. Rodrígues-Pascua. 2005. Lake level change, climate, and the impact of natural events: The role of seismic and volcanic events in the formation of the Lake Patzcuaro Basin, Michoacán, Mexico. Quatern. Int. 135: 35–46.

Jacob, J. S. and C. T. Hallmark. 1996. Holocene stratigraphy of Cobweb Swamp, a Maya wetland in northern Belize. Geol. Soc. Amer. Bull. 108: 883–891.

Jacobs, B. F. 1982. Modern pollen spectra from surface soil

samples, northern Nayarit, southern Sinaloa, Mexico. J. Arizona-Nevada Acad. Sci. 17: 1–14.

Joblonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314: 102–106.

Kennedy, L. M. and S. P. Horn. 1997. Prehistoric maize cultivation at the La Selva Biological Station, Costa Rica. Biotropica 29: 368–370.

King, J. E. and T. R. Van Devender. 1977. Pollen analysis of fossil packrat middens from the Sonoran Desert. Quatern. Res. 8: 191–204.

Klink, C. A. and A. G. Moreira. 2002. Past and current human occupation, and land use. *In:* P. S. Oliveira and R. J. Marquis (eds.), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. pp. 69–88.

Kurtz, A. C., L. R. Kump, M. A. Arthur, J. C. Zachos, and A. Paytan. 2003. Early Cenozoic decoupling of the global carbon and sulfur cycles. Palaeoceanography 18: 1090.

Lachniet, M. S. and L. Vázquez-Selem. 2005. Last glacial maximum equilibrium line altitudes in the circum-Caribbean (Mexico, Guatemala, Costa Rica, Colombia, and Venezuela). Quatern. Int. 138/139: 129–144.

Langenheim, J. H. 1966. Botanical source of amber from Chiapas, Mexico. Ciencia (Mexico) 24: 201–210.

———, B. L. Hackner, and A. S. Bartlett. 1967. Mangrove pollen at the depositional site of Oligo–Miocene amber from Chiapas, Mexico. Bot. Mus. Leafl. 21: 289–324.

Lewin, R. 1987. The first Americans are getting younger. Science 238: 1230–1232.

Leyden, B. W. 1984. Guatemalan forest synthesis after Pleistocene aridity. Proc. Natl. Acad. Sci. U.S.A. 81: 4856–4859.

———. 2002. Pollen evidence for climatic variability and cultural disturbance in the Maya lowlands. Ancient Mesoamerica 13: 85–101.

———, M. Brenner, D. A. Hodell, and J. H. Curtis. 1994. Orbital and internal forcing of climate on the Yucatán Peninsula for the past ca. 36 ka. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 193–210.

——— et al. (+ 5 authors). 1996. A record of long and short-term climatic variation from northwest Yucatán: Cenote San José Chulchaca. *In:* S. L. Fedick (ed.), The Managed Mosaic: Ancient Maya Agriculture and Resource Use. University of Utah Press, Ogden. pp. 30–50.

———, M. Brenner, and B. H. Dahlin. 1998. Cultural and climatic history of Coba, a lowland Maya city in Quintana Roo, Mexico. Quatern. Res. 49: 111–122.

Lourens, L. J. et al. (+ 7 authors). 2005. Astronomical pacing of late Palaeocene to early Eocene global warming events. Nature 435: 1083–1087.

Lowenstein, T. K. and R. V. Demicco. 2006. Elevated Eocene atmosphere CO_2 and its subsequent decline. Science 313: 1928.

Lozano-García, M. S. and B. Ortega-Guerrero. 1994. Palynological and magnetic susceptibility records of Lake Chalco, central Mexico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 177–191.

——— and ———. 1998. Late Quaternary environmental changes of the central part of the Basin of Mexico; Correlation between Texcoco and Chalco basins. Rev. Palaeobot. Palynol. 99: 77–93.

———, ———, M. Caballero Miranda, and J. Urrutia Fucugauchi. 1993. Late Pleistocene and Holocene paleoenvironments of Chalco Lake, central Mexico. Quatern. Res. 40: 332–342.

———, ———, and S. Sosa-Nájera. 2002. Mid- to late-Wisconsin pollen record of San Felipe Basin, Baja California. Quatern. Res. 58: 84–92.

———, Sosa-Nájera, Y. Sugiura, and M. Caballero. 2005. 23,000 years of vegetation history of the upper Lerma, a tropical high-altitude basin in central Mexico. Quatern. Res. 64: 70–82.

——— and L. Vázquez-Selem. 2005. A high-elevation Holocene pollen record from Iztaccíhuatl Volcano, central Mexico. The Holocene 15: 329–338.

——— and M. S. Xelhuantzi-López. 1997. Some problems in the Late Quaternary pollen records of central Mexico: Basins of Mexico and Zacapú. Quatern. Int. 43/44: 117–123.

Ludlow-Wiechers, B., L. Almeida-Leñero, and G. Islebe. 2005. Paleoecological and climatic changes of the Upper Lerma Basin, central Mexico during the Holocene. Quatern. Res. 64: 318–332.

Magallón-Puebla, S. and S. R. S. Cevallos-Ferriz. 1993. A fossil earthstar (Geasteraceae; Gastromycetes) from the late Cenozoic of Puebla, Mexico. Amer. J. Bot. 80: 1162–1167.

——— and S. R. S. Cevallos-Ferriz. 1994a. Latest occurrence of the extinct genus *Cedrelospermum* (Ulmaceae) in North America: *Cedrelospermum manchesteri* from Mexico. Rev. Palaeobot. Palynol. 81: 115–128.

——— and ———. 1994b. *Eucommia constans* n. sp. fruits from upper Cenozoic strata of Puebla, Mexico: Morphological and anatomical comparison with *Eucommia ulmoides* Oliver. Int. J. Pl. Sci. 155: 80–95.

Mark, B. G. et al. (+ 5 authors). 2005. Tropical snowline changes at the last glacial maximum: A global assessment. Quatern. Int. 138/139: 168–201.

Markgraf, V. 1989. Paleoclimates in Central and South America since 18,000 yr B.P. based on pollen and lake-level records. Quatern. Sci. Rev. 8: 1–24.

——— (ed.). 2001. Interhemispheric Climate Linkages. Academic Press, New York.

Marshall, C. R. 2006. Fossil record reveals tropics as cradle and museum. Science 314: 66–67.

Martin, P. S. 1958. A Biogeography of Reptiles and Amphibians in the Gómez Farías Region, Tamaulipas, Mexico. Miscellaneous Publications No. 101. Museum of Zoology, University of Michigan, Ann Arbor.

———. 2005. Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America. University of Cali-

fornia Press, Berkeley.
——— and B. E. Harrell. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology 38: 468–480.
Martin del Pozzo, A. L., D. Córdoba, and J. López. 1997. Volcanic impact on the southern Basin of Mexico during the Holocene. Quatern. Int. 43/44: 181–190.
Martínez-Hernández, E. 1992. Caracterización ambiental del Terciario de la región de Ixtapa, estado de Chiapas—Un enfoque palinoestratigráfico. Revista Univ. Nac. Auton. Mexico Inst. Geol. 10: 54–64.
———, L. Almeida-Leñero, M. Reyes-Salas, and Y. Betancourt-Aguilar. 1980. Estudio palinológico para la determinación de ambientes en la cuenca Fuentes–Río Escondido (Cretácico Superior), region de Piedras Negras, Coahuila. Revista Univ. Nac. Auton. Mexico Inst. Geol. 4: 167–185.
———, H. Hernández-Campos, and M. Sánchez-López. 1980. Palinología del Eoceno en el noreste de México. Revista Univ. Nac. Auton. Mexico Inst. Geol. 4: 155–166.
——— and E. Ramirez-Arriaga. 1999. Palinoestratigrafía de la región de Tepexi de Rodríguez, Puebla, México—Implicaciones cronoestratigráficas. Revista Mex. Ci. Geol. 16: 187–207.
Matheny, R. T. 1976. Maya lowland hydraulic systems. Science 193: 639–646.
McPhee, J. 1980. Basin and Range. Farrar, Straus, and Giroux, New York.
McVaugh, R. 1943. The vegetation of the granitic flat-rocks of southeastern United States. Ecol. Monogr. 13: 120–166.
Medus, J. and L. Almeida-Leñero. 1982. Des normapolles du Crétacé Supérieur de Piedras Negras (Coahuila, Mexique). Geobios 15: 225–229.
Meggers, B. J. and C. Evans. 1983. Lowland South America and the Antilles. *In:* J. D. Jennings (ed.), Ancient South America. W. H. Freeman, San Francisco. pp. 287–335.
Metcalfe, S. E. 1995. Holocene environmental change in the Zacapú Basin, Mexico: A diatom-based record. The Holocene 5: 196–208.
———. 1997. Palaeolimnological records of climate change in Mexico—frustrating past, promising future? Quatern. Int. 43/44: 111–116.
———. 2006. Late Quaternary environments of the northern deserts and central Transvolcanic Belt of Mexico. *In:* A. Graham (ed.), The Biogeography of Latin America—Causes and Effects. Ann. Missouri Bot. Gard. 93: 258–273.
——— et al. (+ 6 authors). 2007. Long and short-term change in Pátzcuaro Basin, central Mexico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 247: 272–295.
———, A. Bimpson, A. J. Courtice, S. L. O'Hara, and D. M. Taylor. 1997. Climate change at the monsoon/westerly boundary in northern Mexico. J. Paleolimnol. 17: 155–171.
———, S. L. O'Hara, M. Caballero, and S. J. Davies. 2000. Records of Late Pleistocene–Holocene climatic change in Mexico—A review. Quatern. Sci. Rev. 19: 699–721.
———, A. Say, S. Black, R. McCulloch, and S. L. O'Hara. 2002. Wet conditions during the last glaciation in the Chihuahuan Desert, Alta Babicora Basin, Mexico. Quatern. Res. 57: 91–101.
———, F. A. Street-Perrott, R. A. Perrott, and D. D. Harkness. 1991. Palaeolimnology of the Upper Lerma Basin, central Mexico: A record of climatic change and anthropogenic disturbance since 11,600 yr B.P. Paleolimnology 5: 197–218.
——— et al. (+ 5 authors). 1989. Late Holocene human impact on lake basins in central Mexico. Geoarchaeology 4: 119–141.
Meyer, E. R. 1973. Late-Quaternary paleoecology of the Cuatro Ciénegas Basin, Coahuila, Mexico. Ecology 54: 982–995.
Mirambell, L. 1978. Tlapacoya: A late Pleistocene site in Central Mexico. *In:* A. L. Bryan (ed.), Early Man in America, from a Circum-Pacific Perspective. Dept. Anthropol. Univ. Alberta, Occas. Papers 1: 1–327.
Miranda, F. 1963. Two plants from the amber of the Simojovel, Chiapas, Mexico, area. J. Paleontol. 37: 611–614.
——— and A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31: 313–333.
Moore, M. J. and R. K. Jansen. 2006. Molecular evidence for the age, origin, and evolutionary history of the American desert plant genus *Tiquilia* (Boraginaceae). Molec. Phylogen. Evol. 39: 668–687.
Moran, K. et al. (+ 36 authors). 2006. The Cenozoic palaeoenvironment of the Arctic Ocean. Nature 441: 601–605.
Muhs, D. R., K. R. Simmons, and B. Steinke. 2002. Timing and warmth of the Last Interglacial period: New U-series evidence from Hawaii and Bermuda and a new fossil compilation for North America. Quatern. Sci. Rev. 21: 1355–1383.
Mullerried, F. K. G. 1938. Acerca del material colectado en el municipio de Tlacolulan, estado de Veracruz. Bol. Soc. Geol. Mex. 10: 203–206.
Murillo de Nava, J. M., D. S. Gorsline, G. A. Goodfriend, V. K. Vlasov, and R. Cruz-Orozco. 1999. Evidence of Holocene climatic changes from aeolian deposits in Baja California Sur, Mexico. Quatern. Int. 56: 141–154.
Musgrove, M. et al. (+ 6 authors). 2001. Geochronology of late Pleistocene to Holocene speleothems from central Texas: Implications for regional paleoclimate. Geol. Soc. Amer. Bull. 113: 1532–1543.
Newton, A. J. et al. (+ 5 authors). 2005. Late Quaternary volcanic record from lakes of Michoacán, central Mexico. Quatern. Sci. Rev. 24: 91–104.
Nunes, F. and R. D. Norris. 2006. Abrupt reversals in ocean overturning during the Palaeocene/Eocene warm period. Nature 439: 60–63.
Núñez, A. L., M. Grosjean, and I. Cartajena. 2002. Human

occupations and climate change in the Puna de Atacama, Chile. Science 298: 821–824.

O'Hara, S. L., F. A. Street-Perrott, and T. P. Burt. 1993. Accelerated soil erosion around a Mexican highland lake caused by prehispanic agriculture. Nature 362: 48–51.

——— and S. E. Metcalfe. 1997. The climate of Mexico since the Aztec Period. Quatern. Int. 43/44: 25–31.

Ohngemach, D. 1973. Analisis polinico de los sedimentos del Pleistoceno reciente y del Holoceno en la region Puebla-Tlaxcala. Comun. Proyecto Puebla-Tlaxcala 7: 47–49.

———. 1977. Pollen sequence of the Tlaloqua crater (La Malinche volcano, Tlaxcala, Mexico). Bol. Soc. Bot. Mex. 36: 33–40.

——— and H. Straka (mit einem Anhang von W. Lauer). 1983. Beiträge zur vegetations—und klimageschichte im gebiet von Puebla–Tlaxcala pollenanalysen im Mexiko–Projekt. Franz Steiner Verlag, Wiesbaden, Germany.

Ortega, B., C. Caballero, S. Lozano, I. Israde, and G. Vilaclara. 2002. 52,000 years of environmental history in Zacapú Basin, Michoacán, Mexico: The magnetic record. Earth Planet. Sci. Lett. 202: 663–675.

Orvis, K. H. 1998. Modern surface pollen from three transects across the southern Sonoran Desert margin, northwestern Mexico. Palynology 22: 197–211.

——— and S. P. Horn. 2000. Quaternary glaciers and climate on Cerro Chirripó, Costa Rica. Quatern. Res. 54: 24–37.

Paez, M. M., A. R. Prieto, and M. V. Mancini. 1999. Fossil pollen from Los Todos locality: A record of the Late Glacial transition in the extra-Andean Patagonia. Quatern. Int. 53/54: 69–75.

Pagani, M. et al. (+ 8 authors). 2006a. Arctic hydrology during global warming at the Palaeocene/Eocene thermal maximum. Nature 442: 671–675.

———, K. Caldeira, D. Archer, and J. C. Zachos. 2006b. An ancient carbon mystery. Science 314: 1556–1557.

Palacios, D., G. Parrilla, and J. L. Zamorano. 1999. Paraglacial and postglacial debris flows on a Little Ice Age terminal moraine: Jamapa glacier, Pico de Orizaba (Mexico). Geomorphology 28: 95–118.

Palacios Chávez, R. 1977. Lluvia de polen moderno en diferentes habitats del Valle de México. Bol. Soc. Bot. Mex. 36: 45–69.

——— and J. Rzedowski. 1993. Estudio palinologico de las flores fosiles del Mioceno inferior y principios del Mioceno medio de la region de Pichucalco, Chiapas, Mexico. Acta Bot. Mex. 24: 1–96.

Pälike, H. et al. (+ 8 authors). 2006. The heartbeat of the Oligocene climate system. Science 314: 1894–1898.

Pearsall, D. M. 2002. Maize is *still* ancient in prehistoric Ecuador: The view from Real Alto, with comments on Staller and Thompson. J. Archaeol. Sci. 29: 51–55.

Peterson, G. L. and P. L. Abbott. 1979. Mid-Eocene climatic change, southwestern California and northwestern Baja California. Palaeogeogr. Palaeoclimatol. Palaeoecol. 26: 73–87.

Piperno, D. R. 2003. A few kernels short of a cob: On the Staller and Thompson late entry scenario for the introduction of maize into northern South America. J. Archaeol. Sci. 30: 831–836.

———. 2006. Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists. Altamira Press (Division of Rowman & Littlefield Publishing Group), Lanham, MD.

——— and K. V. Flannery. 2001. The earliest archaeological maize (*Zea mays* L.) from highland Mexico: New accelerator mass spectrometry dates and their implications. Proc. Natl. Acad. Sci. U.S.A. 98: 2101–2103.

——— and D. M. Pearsall. 1998. The Origins of Agriculture in the Lowland Neotropics. Academic Press, London.

———, A. J. Ranere, I. Holst, and P. Hansell. 2000. Starch grains reveal early root crop horticulture in the Panamanian tropical forest. Nature 407: 894–897.

——— and K. E. Stothert. 2003. Phytolith evidence for early Holocene *Cucurbita* domestication in southwest Ecuador. Science 299: 1054–1057.

——— and H.-D. Sues. 2005. Dinosaurs dined on grass. Science 310: 1126–1128.

Pitulko, V. V. et al. (+ 5 authors). 2004. The Yana RHS site: Humans in the Arctic before the Last Glacial Maximum. Science 303: 52–56.

Poinar, G., Jr. 2002. Fossil palm flowers in Dominican and Mexican amber. J. Linn. Soc., Bot. 138: 57–61.

Polyak, V. J., J. C. Cokendolpher, R. A. Norton, and Y. Asmerom. 2001. Wetter and cooler late Holocene climate in the southwestern United States from mites preserved in stalagmites. Geology 29: 643–646.

Pope, K. O. et al. (+ 6 authors). 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. Science 292: 1370–1373.

Potzger, J. E. and B. C. Tharp. 1943. Pollen record of Canadian spruce and fir from Texas bog. Science 98: 584–585.

——— and ———. 1947. Pollen profile from a Texas bog. Ecology 28: 274–280.

——— and ———. 1954. Pollen study of two bogs in Texas. Ecology 35: 462–466.

Prasad, V., C. A. E. Strömberg, H. Alimohammadian, and A. Sahni. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. Science 310: 1177–1180.

Quilter, J. et al. (+ 5 authors). 1991. Subsistence economy of El Paraíso, an early Peruvian site. Science 251: 277–283.

Ramírez, J. L. and S. R. S. Cevallos-Ferriz. 2002. A diverse assemblage of Anacardiaceae from Oligocene sediments, Tepexi de Rodríguez, Puebla, Mexico. Amer. J. Bot. 89: 535–545.

———, ———, and A. Silva-Pineda. 2000. Reconstruction of the leaves of two new species of *Pseudosmodingium* (Anacardiaceae) from Oligocene strata of Puebla, Mexico. Int. J. Pl. Sci. 161: 509–519.

Ramírez-Arriaga, E., E. Martínez-Hernández, and M. B. Prámparo. 2005. Palynomorph assemblages of the Cua-

yuca Formation (Paleogene), Puebla, southern Mexico. Part 1. Trilete spores, monolete spores and gymnosperm pollen. Ameghiniana 42: 567–578.

Ravelo, A. C., D. H. Andreasen, M. Lyle, A. Lyle, and M. W. Wara. 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. Nature 429: 263–267.

Rhode, D. 2002. Early Holocene juniper woodland and chaparral taxa in the central Baja California Peninsula, Mexico. Quatern. Res. 57: 102–108.

Romano, A. 1964. Restos humanos precerámicos. *In:* 35th Congr. Internat. Americanistas, Mexico, 1962. Actas Mem. 3: 61–64. [English translation: Preceramic human remains. *In:* D. Stewart (ed.), Handbook of Middle American Indians, Vol. 9, Physical Anthropology. University of Texas Press, Austin. pp 22–34.]

Roosevelt, A. C. et al. (+ 14 authors). 1996. Paleoindian cave dwellers in the Amazon: The peopling of the Americas. Science 272: 373–384.

Rosenmeier, M. F., D. A. Hodell, M. Brenner, and J. H. Curtis. 2002. A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Petén, Guatemala. Quatern. Res. 57: 183–190.

Royer, D. L. and P. Wilf. 2006. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. Int. J. Pl. Sci. 167: 11–18.

Rue, D. J. 1987. Early agriculture and early postclassic Maya occupation in western Honduras. Nature 326: 285–286.

Ruiz Martínez, M. A. and J. Werner. 1997. Research into the Quaternary sediments and climatic variations in NE Mexico. Quatern. Int. 43/44: 145–151.

Rust, W. F. and R. J. Sharer. 1988. Olmec settlement data from La Venta, Tabasco, Mexico. Science 242: 102–104.

Rzedowski, J. 1978. Vegetación de México. Editorial Limusa, México, D.F.

———. 1996. Analisis preliminar de la flora vascular de los bosques mesofilos de montaña de México. Acta Bot. Mex. 35: 25–44.

Sancetta, C. 1995. Diatoms in the Gulf of California: Seasonal flux patterns and the sediment record for the last 15,000 years. Paleoceanography 10: 67–84.

Schmitz, B., J. Sundquist, and F. P. Andreasson (eds.). 2000. Early Paleogene Warm Climates and Biosphere Dynamics. GFF (Geologiska Föreningen), Vol. 122. Geological Society of Sweden, Stockholm.

Sears, P. B. 1951. Pollen profiles and culture horizons in the Basin of Mexico. TAX: The Civilizations of Ancient America, Vol. 1, Proceedings of the 29th International Congress of Americanists (1951). University of Chicago Press, Chicago. pp. 57–61.

———. 1952. Palynology in southern North America. I: Archeological horizons in the basins of Mexico. Geol. Soc. Amer. Bull. 63: 241–254.

———. 1955. Palynology in southern North America. Introduction and acknowledgments. Geol. Soc. Amer. Bull. 66: 471–473.

——— and K. H. Clisby. 1955. Palynology in southern North America. Part IV: Pleistocene climate in Mexico. Geol. Soc. Amer. Bull. 66: 521–530.

Segerstrom, K. 1961. Geología del suroeste del estado de Hidalgo y del noreste del estado de México. Bol. Asoc. Mex. Geol. Petrol. 13: 147–168.

Serlin, B. S., T. Delevoryas, and R. Weber. 1980–1981. A new conifer pollen cone from the Upper Cretaceous of Coahuila, Mexico. Rev. Palaeobot. Palynol. 31: 241–248.

Sharp, A. J. 1966. Some aspects of Mexican phytogeography. Ciencia (Mexico) 24: 5–6.

Shaw, C. A. and H. G. McDonald. 1987. First record of giant anteater (*Xenarthra*, Myrmecophagidae) in North America. Science 236: 186–188.

Siebe, C., J. L. Macías, M. Abrams, S. Rodríguez, R. Castro, and H. Delgado. 1995. Quaternary explosive volcanism and pyroclastic deposits in east central Mexico: Implications for future hazards. Geological Society of America Annual Meeting, Field Trip Guide Book.

———, M. Abrams, J. L. Macías, and J. Obenholzer. 1996. Repeated volcanic disasters in prehispanic time at Popocatépetl, central Mexico: Past key to future? Geology 24: 399–402.

———, P. Schaaf, and J. Urrutia-Fucugauchi. 1999. Mammoth bones embedded in a late Pleistocene lahar from Popocatépetl volcano, near Tocuila, central Mexico. Geol. Soc. Amer. Bull. 111: 1550–1562.

Sluijs, A. et al. (+ 14 authors and the Expedition 302 Scientists). 2006. Subtropical Arctic Ocean temperatures during the Paleocene/Eocene thermal maximum. Nature 441: 610–613.

Sluyter, A. 1997. Regional, Holocene records of the human dimension of global change: Sea-level and land-use change in prehistoric Mexico. Global Planet. Change 14: 127–146.

Smith, B. D. 1997. The initial domestication of *Cucurbita pepo* in the Americas 10,000 years ago. Science 276: 932–934.

Spaulding, W. G. 1991. A middle Holocene vegetation record from the Mojave Desert of North America and its paleoclimatic significance. Quatern. Res. 35: 427–437.

Staller, J. E. and R. G. Thompson. 2002. A multidisciplinary approach to understanding the initial introduction of maize into coastal Ecuador. J. Archaeol. Sci. 29: 33–50.

Stoll, H. M. 2006. The Arctic tells its story. Nature 441: 579–581.

Straka, H. and D. Ohngemach. 1989. Late Quaternary vegetation history of the Mexican highland. Pl. Syst. Evol. 162: 115–132.

Sun, J. and T. Liu. 2006. The age of the Taklimakan Desert. Science 312: 1621.

Svensen, H. et al. (+ 6 authors). 2004. Release of methane from a volcanic basin as a mechanism for initial Eocene global warming. Nature 429: 542–545.

Tarasov, L. and W. R. Peltier. 2005. Arctic freshwater forcing of the Younger Dryas cold reversal. Nature 435: 662–665.

Tchakerian, V. P. and N. Lancaster. 2002. Late Quaternary arid/humid cycles in the Mojave Desert and western Great Basin of North America. Quatern. Sci. Rev. 21: 799–810.

Tejero-Diez, J. D., M. Reyes-Salas, and E. Martínez-Hernández. 1988. Lluvia de pollen moderno de un gradiente altitudinal con vegetación templada en el municipio of Ocuilán, Edo. de México. Palynológica et Palaeobotánica (IPN, México) 1: 61.

Telford, R. J., P. Barker, S. Metcalfe, and A. Newton. 2004. Lacustrine responses to tephra deposition: Examples from Mexico. Quatern. Sci. Rev. 23: 2337–2353.

Tomasini-Ortiz, A. C. and E. Martínez-Hernández. 1984. Palinología del Eoceno–Oligoceno de Simojovel, Chiapas. Paleontol. Mex. 50: 1–49.

Tripati, A. and H. Elderfield. 2005. Deep-sea temperatures and circulation changes at the Paleocene–Eocene thermal maximum. Science 308: 1894–1898.

Utescher, T. and V. Mosbrugger. 2007. Eocene vegetation patterns reconstructed from plant diversity—A global perspective. Palaeogeogr. Palaeoclimatol. Palaeoecol. 247: 243–271.

Van Devender, T. R. 1985. Climatic cadences and the composition of Chihuahuan Desert communities: The Late Pleistocene packrat midden record. *In:* J. Diamond and T. J. Case (eds.), Community Ecology. Harper & Row, New York. pp. 285–299.

———. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. *In:* J. L. Betancourt, T. R. Van Devender, and P. S. Martin (eds.), Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson. pp. 134–165.

——— and T. L. Burgess. 1985. Late Pleistocene woodlands in the Bolsón de Mapimí: A refugium for the Chihuahuan Desert biota? Quatern. Res. 24: 346–353.

———, ———, R. S. Felger, and R. M. Turner. 1990. Holocene vegetation of the Hornaday Mountains of northwestern Sonora, Mexico. Proc. San Diego Soc. Nat. Hist. 2: 1–19.

———, ———, J. C. Piper, and R. M. Turner. 1994. Paleoclimatic implications of Holocene plant remains from the Sierra Bacha, Sonora, Mexico. Quatern. Res. 41: 99–108.

Vázquez-Selem, L. 1997. Late Quaternary glaciations of Téyotl volcano, central Mexico. Quatern. Int. 43/44: 67–73.

Velasco de León, P. and S. R. S. Cevallos-Ferriz. 2000. Leaves of *Cercocarpus mixteca* n. sp. (Rosaceae) from Oligocene sediments, near Tepexi de Rodríguez, Puebla. Rev. Palaeobot. Palynol. 111: 285–294.

———, ———, and A. Silva-Pineda. 1998. Leaves of *Karwinskia axamilpense* sp. nov. (Rhamnaceae) from Oligocene sediments, near Tepexi de Rodríguez, Puebla, Mexico. Can. J. Bot. 76: 410–419.

Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771–780.

Watts, W. A. and J. P. Bradbury. 1982. Paleoecological studies at Lake Pátzcuaro on the west-central Mexican Plateau and at Chalco in the Basin of Mexico. Quatern. Res. 17: 56–70.

Weber, R. 1972. La vegetación Maastrichtiana de la Formación Olmos de Coahuila, México. Bol. Soc. Geol. Mexicana 33: 5–19.

———. 1973. *Salvinia coahuilensis* Nov. Sp. del Cretacico Superior de Mexico. Ameghiniana 10: 173–190.

———. 1975. *Aachenia knoblochi* N. Sp., an interesting conifer from the Upper Cretaceous Olmos Formation of northeastern Mexico. Palaeontographica, Abt. B, Paläophytol. 152: 76–83.

———. 1976. *Dorfiella auriculata* F. Gen. Nov., Sp. Nov., un genero nuevo de helechos acuaticos del Cretácico Superior de México. Bol. Asoc. Latinoamer. Paleobot. Palin. 3: 1–13.

Webster, J. W. et al. (+ 6 authors). 2007. Stalagmite evidence from Belize indicating significant droughts at the time of Preclassic abandonment, the Maya Hiatus, and the Classic Maya collapse. Palaeogeogr. Palaeoclimatol. Palaeoecol. 250: 1–17.

Weeks, A., D. C. Daly, and B. B. Simpson. 2005. The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. Molec. Phylogen. Evol. 35: 85–101.

Wells, P. V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science 153: 970–975.

Wendt, T. 1993. Composition, floristic affinities, and origin of the canopy tree flora of the Mexican Atlantic slope rain forests. *In:* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa (eds.), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, Oxford, U.K. pp. 595–680.

Westgate, J. W. and C. T. Gee. 1990. Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 78: 163–177.

Wheeler, E. A. and T. M. Lehman. 2005. Upper Cretaceous–Paleocene conifer woods from Big Bend National Park, Texas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 226: 233–258.

White, S. E. 1962. Late Pleistocene glacial sequence for the west side of Iztaccihuatl, Mexico. Geol. Soc. Amer. Bull. 73: 935–958.

———. 1987. Quaternary glacial stratigraphy and chronology of Mexico. Quatern. Sci. Rev. 5: 201–205.

Xelhuantzi Lopez, M. S. 1994a. Estudio palinológico de cuatro sitios ubicados en la Cuenca de Zacapú: Fondo de ciénega, pantano interno y Loma Alta. Cuad. Estud. Michoacános 6: 81–93.

———. 1994b. Determinación palinológica del paleoambiente Holocenico en la parte norte del estado de Michoacán. Bol. Soc. Bot. Mex. 54: 251–265.

Xiang, Q.-Y, D. E. Soltis, and P. S. Soltis. 1998. The eastern Asian and eastern and western North American floristic disjunction: Congruent phylogenetic patterns in seven diverse genera. Molec. Phylogen. Evol. 10: 178–190.

———, ———, ———, S. R. Manchester, and D. J. Crawford. 2000. Timing the eastern Asian–eastern North American floristic disjunction: Molecular clock corroborates paleontological estimates. Molec. Phylogen. Evol. 15: 462–472.

Zachos, J. C. et al. (+ 7 authors). 2003. A transient rise in tropical sea surface temperature during the Paleocene–Eocene Thermal Maximum. Science 302: 1551–1554.

ADDITIONAL REFERENCES/GENERAL READINGS/ ELECTRONIC ADDRESSES

Adams, R. E. W., W. E. Brown Jr., and T. Patrick Culbert. 1981. Radar mapping, archeology, and ancient Maya land use. Science 213: 1457–1463.

Aldenderfer, M. 1999. The Pleistocene/Holocene transition in Peru and its effects upon human use of the landscape. Quatern. Int. 53/54: 11–19.

———. 2003. Moving up in the world. Amer. Sci. 91: 542–549.

Antaramian, E. and E. Múzquiz-Iribe. 1997. Recent climate trends in Michoacán. Quatern. Int. 43/44: 33–42.

Arundel, S. T. 2002. Modeling climate limits of plants found in Sonoran Desert packrat middens. Quatern. Res. 58: 112–121.

Bawaya, M. 2005. Maya archaeologists turn to the living to help save the dead. Science 309: 1317–1318.

Borrero, L. A. 1998. Human dispersal and climatic conditions during late Pleistocene times in Fuego-Patagonia. Quatern. Int. 53/54: 93–99.

Brenner, M. et al. (+ 5 authors). 2001. Abrupt climate change and pre-Colombian cultural collapse. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 87–103.

Bristol Research Initiative for the Dynamic Global Environment, University of Bristol School of Geographical Sciences. http://www.bridge.bris.ac.uk/resources/Databases/LGM. [LGM Tropical Terrestrial Data Synthesis; PMIP-sponsored SNOWLINE Database.]

Butzer, K. W. 1993. No Eden in the New World. Nature 362: 15–17.

Byrne, R. 1982. Preliminary pollen analysis of Deep Sea Drilling Project Leg 64, Hole 480, cores 1–11. *In:* J. R. Curray et al. (eds.), Initial Reports of the Deep Sea Drilling Project 64: 1225–1237.

Cavillo-Canadell, L. and S. R. S. Cevallos-Ferriz. 2002. *Inga* and *Pithecellobium* en el Terciario de México. Ponencias, Sociedad Mexicana de Paleontología, VIII Congreso Nacional de Paleontología (Guadalajara, México): 37.

Cervantes-Borja, J. F., M. Meza-Sánchez, and G. Alfaro-Sánchez. 1997. Sedimentological characterization of palaeosoils in the northern part of the Basin of Mexico. Quatern. Int. 43/44: 75–86.

Cevallos-Ferriz, S. R. S. and O. S. Ricalde-Moreno. 1995. Palmeras fósiles del norte de México. Anales Inst. Biol. Univ. Nac. Auton. Mexico, Bot. 66: 37–106.

Cieslak, T. et al. (+ 8 authors). 2005. Phylogenetic analysis of *Pinguicula* (Lentibulariaceae): Chloroplast DNA sequences and morphology support several geographically distinct radiations. Amer. J. Bot. 92: 1723–1736.

Clarke, G., D. Leverington, J. Teller, and A. Dyke. 2003. Superlakes, megafloods, and abrupt climate change. Science 301: 922–923.

Coccioni, R., S. Monechi, and M. R. Rampino. 2007. Cretaceous–Paleogene boundary events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 255: 1–3.

Conserva, M. E. and R. Byrne. 2002. Late Holocene vegetation change in the Sierra Madre Oriental of central Mexico. Quatern. Res. 58: 122–129.

Dalton, R. 2005. Caveman DNA hints at map of migration. Nature 436: 162.

Estrada-Ruíz, E. and S. R. S. Cevallos-Ferriz. 2002. Estructuras reproductivas del orden Arales en la Formación Cerro del Pueblo (Cretácico, Campaniano) de Coahuila, México. Ponencias, Sociedad Mexicana de Paleontología, VIII Congreso Nacional de Paleontología (Guadalajara, México): 45.

Fedoroff, N. V. 2003. Prehistoric GM corn. Science 302: 1158–1159.

Ferrusquía-Villafranca, I. and L. I. González-Guzmán. 2005. Northern Mexico's landscape, Part II: The biotic setting across time. *In:* J. L. E. Cartron, G. Ceballos, and R. S. Felger (eds.), Biodiversity, Ecosystems, and Conservation in Northern Mexico. Oxford University Press, Oxford, U.K. pp. 39–51.

François, L., M. Ghislain, D. Otto, and A. Micheels. 2006. Late Miocene vegetation reconstruction with the CARAIB model. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238: 302–320. [Drier vegetation expands since the late Miocene.]

Fuentes, E. R. and M. R. Muñoz. 1995. The human role in changing landscapes in central Chile: Implications for intercontinental comparisons. *In:* M. T. Kalin Arroyo, P. H. Zedler, and M. D. Fox (eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Ecological Studies 108. Springer Verlag, Berlin. pp. 401–417.

García, A., M. Zárate, and M. Mercedes Paez. 1999. The Pleistocene/Holocene transition and human occupation in the Central Andes of Argentina: Agua de la Cueva locality. Quatern. Int. 53/54: 43–52.

Gingerich, P. D. 2006. Environment and evolution through the Paleocene–Eocene thermal maximum. Trends Ecol. Evol. 21: 246–253.

Gnecco, C. 1999. An archaeological perspective of the Pleistocene/Holocene boundary in northern South America.

Quatern. Int. 53/54: 3–9.
Goman, M., A. Joyce, and R. Mueller. 2005. Stratigraphic evidence for anthropogenically induced coastal environmental change from Oaxaca, Mexico. Quatern. Res. 63: 250–260.
Gómez-Pompa, A., M. F. Allen, S. L. Fedick, and J. J. Jiménez-Osornio (eds.). 2003. The Lowland Maya Area: Three Millennia at the Human-Wildland Interface. Haworth Press, New York.
———, J. Salvador Flores, and V. Sosa. 1987. The "Pet Kot": A man-made tropical forest of the Maya. Interciencia 12: 10–15.
Harley, M. M. 2006. A summary of fossil records for Arecaceae. Bot. J. Linn. Soc. 151: 39–67.
Heusser, L. 1982. Pollen analysis of laminated and homogeneous sediment from the Guaymas Basin, Gulf of Caribbean. *In:* J. R. Curray et al. (eds.), Initial Reports of the Deep Sea Drilling Project 64: 1217–1223.
Hewitt, G. 2000. The genetic legacy of the Quaternary Ice Ages. Nature 405: 907–913.
Hurd, P. D., Jr., R. F. Smith, and J. W. Durham. 1962. The fossiliferous amber of Chiapas, Mexico. Ciencia (Mexico) 21: 107–118.
Jauregui, E. 1997. Climate changes in Mexico during the historical and instrumented periods. Quatern. Int. 43/44: 7–17.
Johannessen, S. and C. A. Hastorf. 1989. Corn and culture in Central Andean prehistory. Science 244: 690–692.
Kerr, R. A. 1990. New view of early Amazonia. Science 248: 1488.
———. 2001. A variable sun and the Maya collapse. Science 292: 1293.
Krajick, K. 1998. Green farming by the Incas? Science 281: 323.
Lambert, J. D. H. and J. T. Arnason. 1982. *Ramón* and Maya ruins: An ecological, not an economic relation. Science 216: 298–299.
Lemonick, M. D. and A. Dorfman. 2006. Who were the first Americans? Time Magazine, March 13: 44–52.
Mann, C. C. 2002. The forgotten people of Amazonia. Science 297: 921.
Martínez-Cabrera, I. and S. R. S. Cevallos-Ferriz. 2002. *Tapirira* (Anacardiaceae) de la Formación El Cien (Oligoceno-Mioceno), Baja California: Consideraciones biogeográficas y evolutivas. Ponencias, Sociedad Mexicana de Paleontología, VIII Congreso Nacional de Paleontología (Guadalajara, México): 63.
Miotti, L. and M. Salemme. 1998. Biodiversity, taxonomic richness and specialists-generalists during late Pleistocene/early Holocene times in Pampa and Patagonia (Argentina, southern South America). Quatern. Int. 53/54: 53–68.
Müller-Beck, H. 1998. The archaeology of the Pleistocene–Holocene transition: Questions, evidences, and the early universal history of women and men. Quatern. Int. 49/50: 3–11.
National Snow and Ice Data Center, World Glacial Inventory. http://www.nsidc.colorado.edu/data/glacier_inventory/. [World Data Center for Glaciology, digital database.]
Nemecek, S. 2000. Who were the first Americans? Sci. Amer. 283: 80–87.
Newton, A. J. and S. E. Metcalfe. 1999. Tephrochronology of the Toluca Basin, central Mexico. Quatern. Sci. Rev. 18: 1039–1059.
Orlove, B. S., J. C. H. Chiang, and M. A. Cane. 2002. Ethnoclimatology in the Andes. Amer. Sci. 90: 428–435.
Osborn, T. J. and K. R. Briffa. 2006. The spatial extent of 20th-century warmth in the context of the past 1200 years. Science 311: 841–844. [...comparison with instrumental temperatures shows the spatial extent of recent warmth to be of greater significance than that during the medieval period.]
Peñalba, M. C. and T. R. Van Devender. 1998. Cambios de vegetación y clima en Baja California, México, durante los ultimos 20,000 años. Geol. Noroeste 2: 21–23.
Pérez-Hernández, B. R. and S. R. S. Cevallos-Ferriz. 2002. Estructura de Phytolaccaceae (Caryophyllales) del Cretácico Superior (Campaniano) de Coahuila, México. Ponencias, Sociedad Mexicana de Paleontología, VIII Congreso Nacional de Paleontología (Guadalajara, México): 69.
Peterson, L. C. and G. H. Haug. 2005. Climate and the collapse of Maya civilization. Amer. Sci. 93: 322–329.
Piperno, D. R. 2001. On maize and the sunflower. Science 292: 2260–2261.
Prous, A. and E. Fogaça. 1999. Archaeology of the Pleistocene–Holocene boundary in Brazil. Quatern. Int. 53/54: 21–41.
Ramírez-Arriaga, E., E. Martínez-Hernández, and M. B. Prámparo. 2005. Palynomorph assemblages of the Cuayuca Formation (Paleogene), Puebla, southern Mexico. Part 1. Trilete spores, monolete spores and gymnosperm pollen. Ameghiniana 42: 567–578.
———, M. B. Prámparo, E. Martínez-Hernández, and A. Valiente-Baunet. 2006. Palynology of the Paleogene Cuayuca Formation (stratotype sections), southern Mexico: Chronostratigraphical and palaeoecological implications. Rev. Palaeobot. Palynol. 141: 259–275.
Rodríguez de la Rosa, R. and S. R. S. Cevallos-Ferriz. 1994. Upper Cretaceous zingiberalean fruits with in situ seeds from southeastern Coahuila, Mexico. Int. J. Pl. Sci. 155: 786–805.
Roosevelt, A. C., R. A. Housley, M. Imazio da Silveira, S. Maranca, and R. Johnson. 1991. Eight millennium pottery from a prehistoric shell midden in the Brazilian Amazon. Science 254: 1621–1624.
Royer, D. L., P. Wilf, D. A. Janesko, E. A. Kowalski, and D. L. Dilcher. 2005. Correlations of climate and plant ecology to leaf size and shape: Potential proxies for the fossil record. Amer. J. Bot. 92: 1141–1151.
Sandoval Montaño, A. 2000. Análisis palinológico y consideraciones paleoambientales de un sondeo en el exlargo de

Texcoco, Cuenca de México. Tesis, Universidad Nacional Autónoma de México, México, D.F.

Sandweiss, D. H. et al. (+ 5 authors). 2001. Variation in Holocene El Niño frequencies: Climate records and cultural consequences in ancient Peru. Geology 29: 603–606.

Sanford, R. L., Jr. and S. P. Horn. 2000. Holocene rain-forest wilderness: A Neotropical perspective on humans as an exotic, invasive species. Proc. USDA Forest Service RMRS-P-15-3: 168–173.

Schlesinger, V. 2002. Animals and Plants of the Ancient Maya: A Guide. University of Texas Press, Austin.

Schönenberger, J. 2005. Rise from the ashes—The reconstruction of charcoal fossil flowers. Trends Pl. Sci. 10: 436–443.

Sirkin, L. 1982. Preliminary palynology of Pleistocene sediments from Deep Sea Drilling Project sites 474 and 479. Initial Reports of the Deep Sea Drilling Project 64: 1211–1215.

Steuber, T., M. Rauch, J.-P. Masse, J. Graff, and M. Malkoc. 2005. Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes. Nature 437: 1341–1344.

Stokstad, E. 2003. "Pristine" forest teemed with people. Science 301: 1645–1646.

Stone, R. 2004. A surprising survival story in the Siberian Arctic. Science 303: 33.

Thien, L. B., A. S. Bradburn, and A. L. Welden. 1982. The woody vegetation of Dzibilchaltun, a Maya archaeological site in northwest Yucatán, Mexico. Middle American Research Institute Occasional Paper 5: 1–24. (With an annotated checklist of plants by A. S. Bradburn and S. P. Darwin.)

Thompson, L. G., M. E. Davis, E. Mosley-Thompson, and K.-b. Liu. 1988. Pre-Incan agricultural activity recorded in dust layers in two tropical ice cores. Nature 336: 763–765.

Toledo, V. M. 1976. Los cambios climaticos del Pleistoceno y sus efectos sobre la vegetacion tropical calida y humeda de México. Tesis, Universidad Nacional Autónoma de México, México, D.F.

———. 1982. Pleistocene changes of vegetation in tropical Mexico. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 93–111.

Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. *In:* J. L. Betancourt, T. R. Van Devender, and P. S. Martin (eds.), Packrat Middens: The Last 40,000 years of Biotic Change. University of Arizona Press, Tucson. pp. 104–133.

Weber, R. and S. R. S. Cevallos-Ferriz. 1944. Perfil actual y perspectivos de la paleobotánica en México. Soc. Bot. Méx. 55: 141–148.

Webster, D. 2003. Adventures of a pioneer Mayanist. Science 299: 204–205. [Ian Graham, 2002, Alfred Maudslay and the Maya, A Biogeography. University of Oklahoma Press, Norman.]

Weissert, H. and S. M. Bernasconi. 2004. An Earth on fire. Nature 428: 130–132.

Wijmstra, T. A. 1968. The identity of *Psilatricolporites* and *Pelliceria*. Acta Bot. Neerl. 17: 114–116.

Chapter 5

THE ANTILLES

CRETACEOUS (144–65 MA)

The oldest vascular plants for the Antilles are from the Early Cretaceous of the Dominican Republic (Smiley, 1982, 2002; Kesler et al., 1991; Table 5.1). The plants are from the Los Ranchos Formation in the Pueblo Viejo mine area north of Santo Domingo and just south of the Cibao Valley (Figs. 5.1, 5.2). They include leaf and bark impressions, and petrified wood of *Brachyphyllum* (also present in the Late Cretaceous Olmos flora of Coahuila, Mexico), *Frenelopsis* (*Pseudofrenelopsis*), *Gleichenites* (*Gleichenoides*), *Phoenicopsis*, *Podozamites*, *Yuccites* (*Pelourdia*), and *Zamites*. Smiley (1982, 2002) considered the Los Ranchos flora Neocomian in age (~144–127 Ma), but the exact age within the Early Cretaceous is not settled (Kesler et al., 1991). At the time, proto-Hispaniola was part of the volcanic island arc located in the isthmian region near southern North America. The site is overlain by marine deposits of Albian age and, therefore, was submerged during its subsequent movement toward the Bahamas Platform. It re-emerged in the middle Eocene. The composition of the flora suggests warm, open, and at least seasonally dry conditions, and the large intact size of some leaves indicates deposition in a shallow marine environment and little transport of the specimens (Smiley, 1982, 2002). The geographic affinities are widespread, typical of Cretaceous assemblages, but are mostly with North America. The flora contains abundant plants, it is important because of its age and location, and it has not been studied since the original discovery.

Floras of Middle Cretaceous age are not common in the Antilles, but there is one microfossil assemblage consisting of 19 identified palynomorphs from the San Adrián Formation in the Yumurí Valley, Matanzas Province, Cuba (Areces-Mallea, 1989). The composition is 35.9% gymnosperms, 29.3% fern spores, and 4.4% tricolpate angiosperm pollen. Like the Maastrichtian Piedras Negras flora of Mexico, gymnosperms are present but there is no bisaccate conifer pollen. The composition suggests warm, seasonally dry climates, and the presence of dinoflagellates indicates deposition in a coastal environment.

Although the Bahamas are north of the region covered in this text, a Middle Cretaceous (Albian or early Cenomanian) palynomorph assemblage from a deep-sea core north of Cat Island (24°54'N, 73°W) is instructive for purposes of comparison (Habib, 1969; Table 5.1). There are a number of pteridophyte spores (ferns and allied groups), gymnosperm pollen, and monocolpate and tricolpate angiosperm pollen like those in other Cretaceous palynofloras known from northern Latin America. However, one difference between the Cat Island and Piedras Negras (Mexico)–San Adrián (Cuba) floras is the relatively large number of bisaccate coniferous pollen grains in the Bahamas assemblage (29.4%). It is most similar to the Middle Cretaceous Patapsco flora of Maryland and generally has North American affinities.

A variety of evidence from paleontology and isotopic geochemistry documents warm marine temperatures in the Early and Middle Cretaceous declining toward the K/T boundary

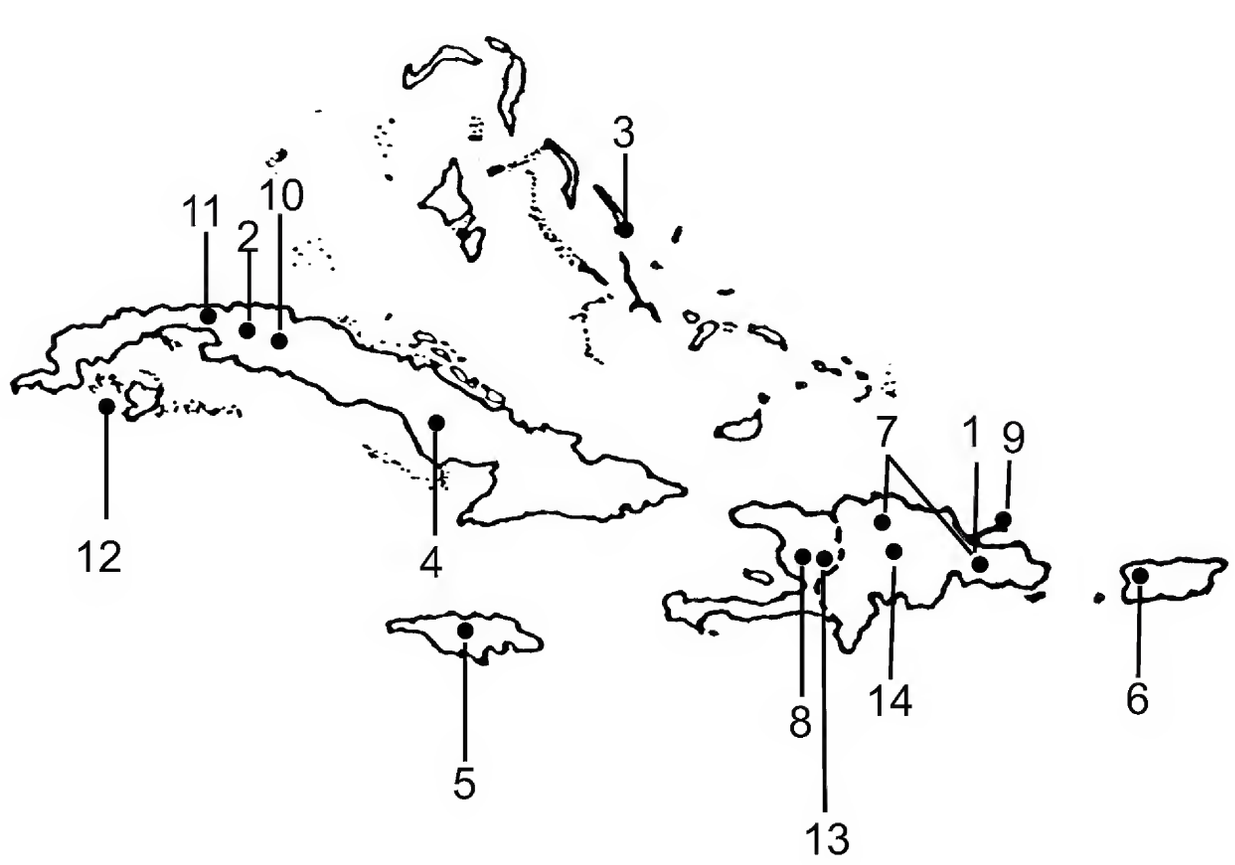


Figure 5.1. Location of fossil floras of the Antilles mentioned in the text. Cretaceous: 1 = Los Ranchos, 2 = San Adrián, Yumurí Valley, 3 = Cat Island; Eocene: 4 = Saramaguacán, 5 = Guys Hill; Oligocene: 6 = San Sebastián; Miocene: 7 = Dominican amber, 8 = Artibonite, 9 = Sánchez; Quaternary: 10 = Chapapote, 11 = S. Las Palmas, 12 = Isla de la Juventud, 13 = Lake Miragoâne, 14 = La Nevera Sabana.

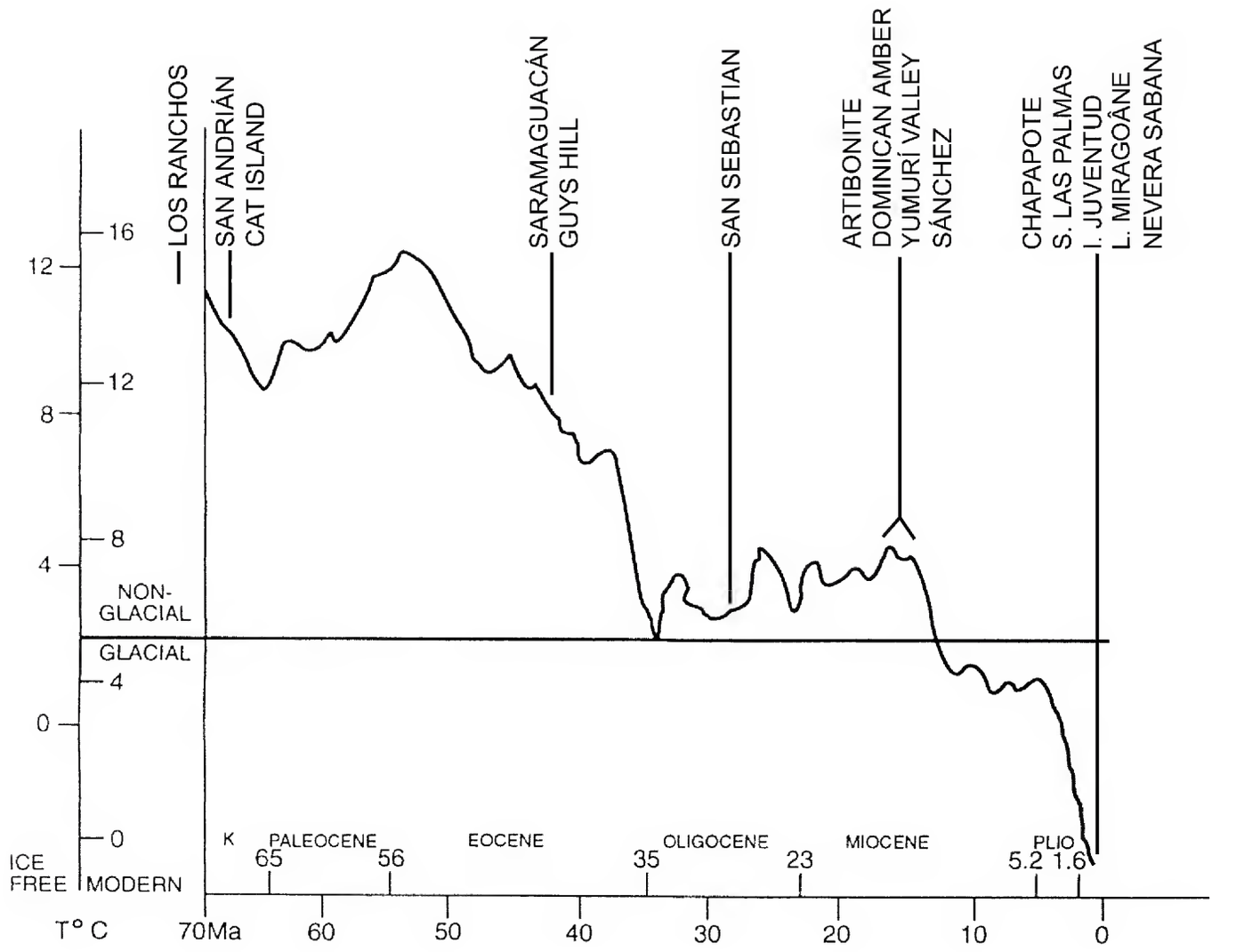


Figure 5.2. Global paleotemperature curve with Late Cretaceous and Tertiary floras of the Antilles.

(Fig. 5.2; MacLeod et al., 2000), and the pattern is paralleled in low-lying terrestrial environments (I: pp. 86–92). Detailed comparisons have not been made to determine if this temperature trend is reflected in the Early Cretaceous Los Ranchos flora of the Dominican Republic, the Middle Cretaceous San Adrián flora of Cuba, the Cat Island flora of the Bahamas, or the Late Cretaceous Olmos and Piedras Negras floras of Mexico. All that can be said about the Cretaceous vegetation of the Antilles is that it conforms to the generalization of widespread, warm-temperate communities; prominent representation of ferns and gymnosperms; minor representation of angiosperms in some Early and Middle Cretaceous floras; and affinities primarily with North America. Studies sufficiently detailed to confirm the presence of specific extant angiosperm lineages (families or genera) have not been made.

EOCENE (54.8–33.7 MA)

The geologic history of the Antilles precluded the development of sustained land vegetation until about the middle Eocene (49–41.3 Ma). At that time, global temperatures were generally high and just declining from the LPTM–EECL, and warm temperate to tropical vegetation was widespread. South America was still an island continent so that except for plants with the potential for long-distance dispersal, the principal affinities of the Paleogene vegetation of the Antilles were with North America. Areces-Mallea (1990) has described the normapolles *Basopollis krutzschi* from the middle Eocene Saramaguacán Formation of Cuba in the Sierra Maraguán (21°19'N, 77°W), province of Camagüey (Fig. 5.3; cf. Fig. 4.4). As noted earlier, this group of plant microfossils defines the Normapolles Province of eastern North America, and the Saramaguacán assemblage has other elements found in the Paleogene of the southeastern United States (Areces-Mallea, 1988; Graham et al., 2000).

The Saramaguacán samples were obtained from a ~30 cm long section of a core from the Sierra Maraguán, and 46 taxa of palynomorphs were identified (Table 5.1; Figs. 5.4–5.10). The fine-grain texture and buff color of the sediments indicate deposition in a swamp or marsh habitat. There are no dinoflagellates in the samples, and neither *Pelliceria*, *Rhizophora*, nor *Brevitricolpites variabilis* were recovered, so it was a freshwater environment beyond marine inundation or tidal influence. Most of the palynomorphs cannot be referred to modern taxa, and only the broadest generalizations can be made about the paleoenvironment. The abundant fern spores, and pollen of the Arecaceae and Bombacaceae, are consistent with the warm temperate to tropical conditions shown on the paleotemperature curve (Fig. 5.2). Among the 46 taxa recognized for the flora, 18 are widespread, 16 are similar to ones present in deposits of similar age in the southeastern United States, and

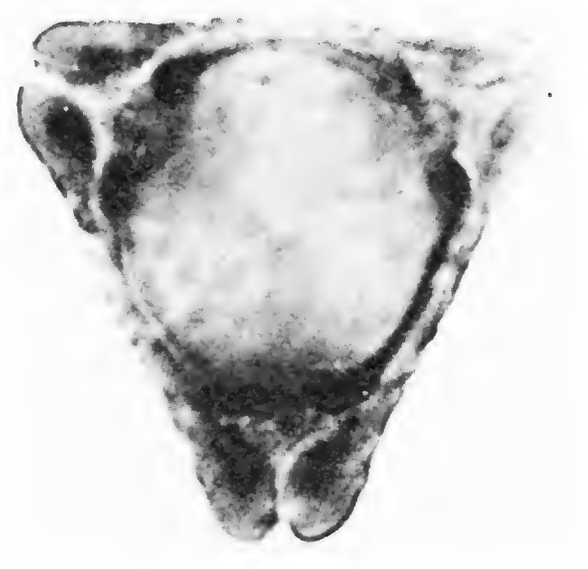
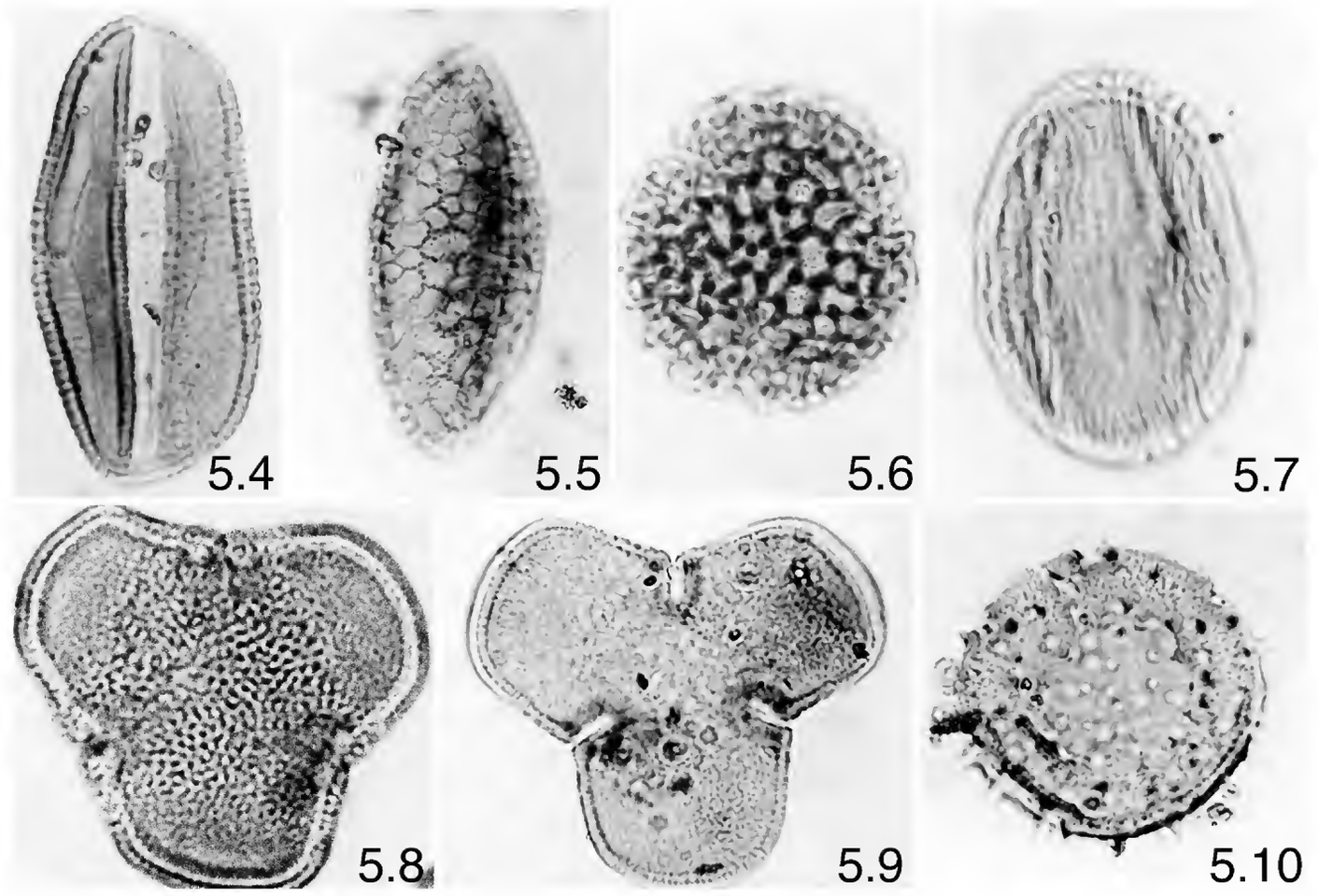


Figure 5.3. *Basopollis krutzschi*, a normapolles pollen from the Paleocene of Cuba. From Areces-Mallea (1990). Used with permission of the author.



Figures 5.4–5.10. Plant microfossils from the middle Eocene Saramaguacán flora of Cuba. 5.4. *Arecipites* sp. 5.5. *Liliacidites* sp. 5.6. *Reticulataepolis* cf. *intergranulata*. 5.7. *Striatricolpites catatumbus*. 5.8. *Bombacacidites* cf. *tilioides*. 5.9. *Bombacacidites* sp. 5.10. *Malvacipollis tschudyi*.

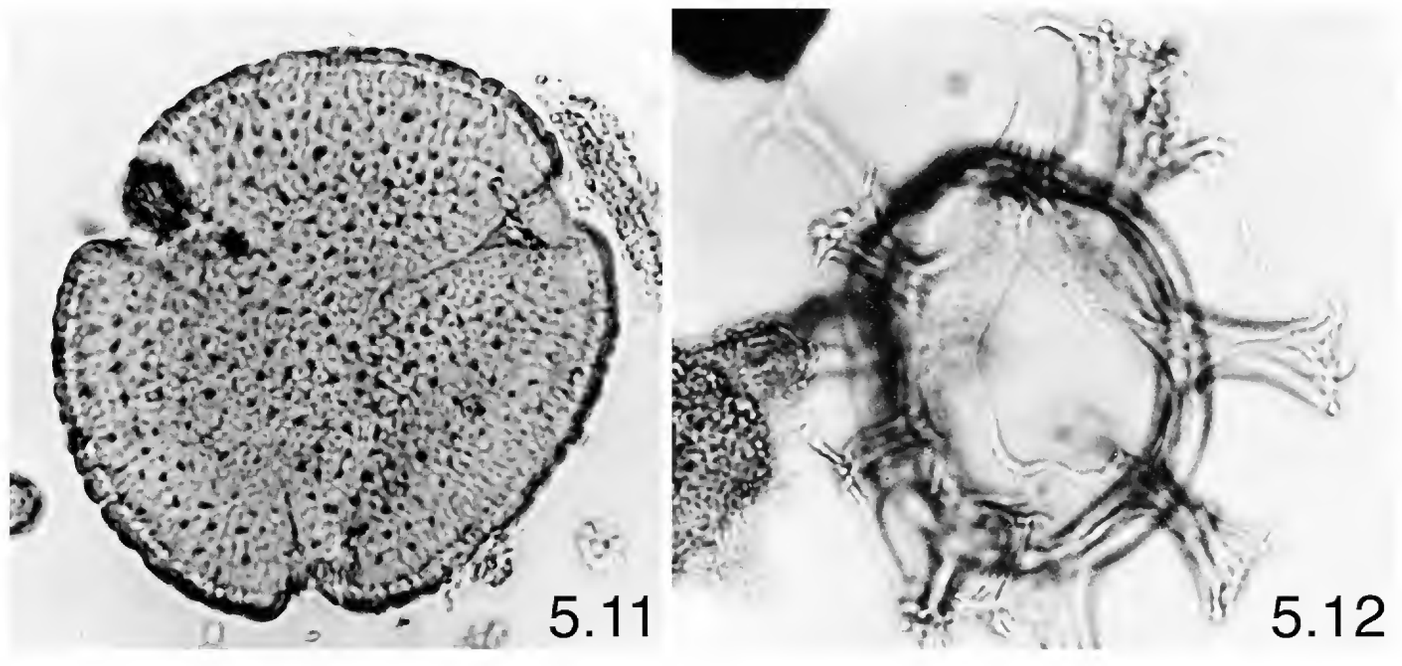
only one (*Retimonocolpites* type 1) is similar to a form described from northern South America.

In Jamaica, the middle Eocene Guys Hill Formation (formerly a member of the Chapelton Formation; Robinson & Mitchell, 1999) contains a small palynoflora approximately the same age as the Saramaguacán, Laredo–Burgos Basin, and the Claiborne floras. It includes dinoflagellate cysts and *Pelliceria* pollen (Figs. 5.11, 5.12) in lignitic lenses, and it was deposited in a coastal brackish-water environment different from that of the freshwater Saramaguacán flora (Graham, 1993). The composition of the flora is given in Table 5.1.

OLIGOCENE (33.7–23.8 MA)

The most extensive fossil plant assemblage in the Antilles is the middle Oligocene San Sebastián flora in the northwestern part of the Central Cordillera of Puerto Rico (~31–22 Ma; Table 5.1). It contains abundant and well-preserved plant megafossils (91 recognized taxa; Hollick, 1928; Graham, 1996), but all are rendered by line drawings that impart a certain uniformity to the illustrations (Fig. 5.13A–E). There are 165 morphological forms of spores and pollen, 44 of which were identified using the reference collection available at the time (~7500 slides representing ~6000 species, compared to the present ~23,500 slides representing ~18,000 species), and 15 had no previously known fossil record. The palynomorphs identified constituted ~84% of the total microfossil flora (Graham & Jarzen, 1969; Figs. 5.14–5.18). It is the only middle Oligocene flora known for the Antilles or, indeed, for all of northern Latin America, depending on the age of the Pie de Vaca flora of Mexico; the megafossils would allow environmental reconstructions on the basis of leaf physiognomy and CLAMP analysis as well as by the modern analog (NLR) method; and the plate tectonic history is now sufficiently well established to provide a sound geologic context. Neither the microfossils nor the megafossils have been revised since the original studies.

The San Sebastián flora was deposited during a time when the modern plant formations of northern Latin America were



Figures 5.11, 5.12. Plant microfossils from the middle Eocene Guys Hill Formation, Jamaica. 5.11. *Psilatricolporites crassus* (*Pelliceria*). 5.12. Dinoflagellate.

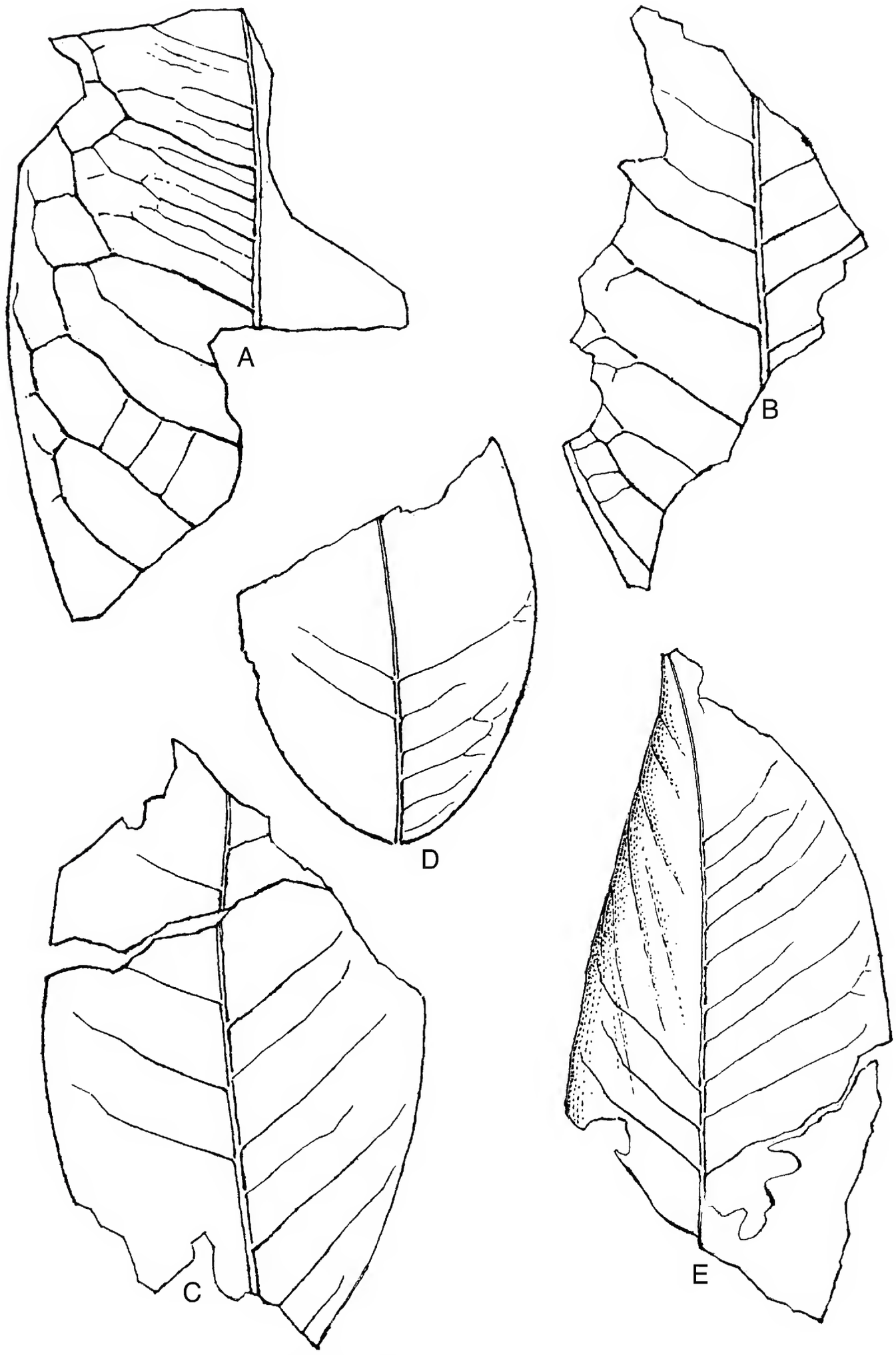
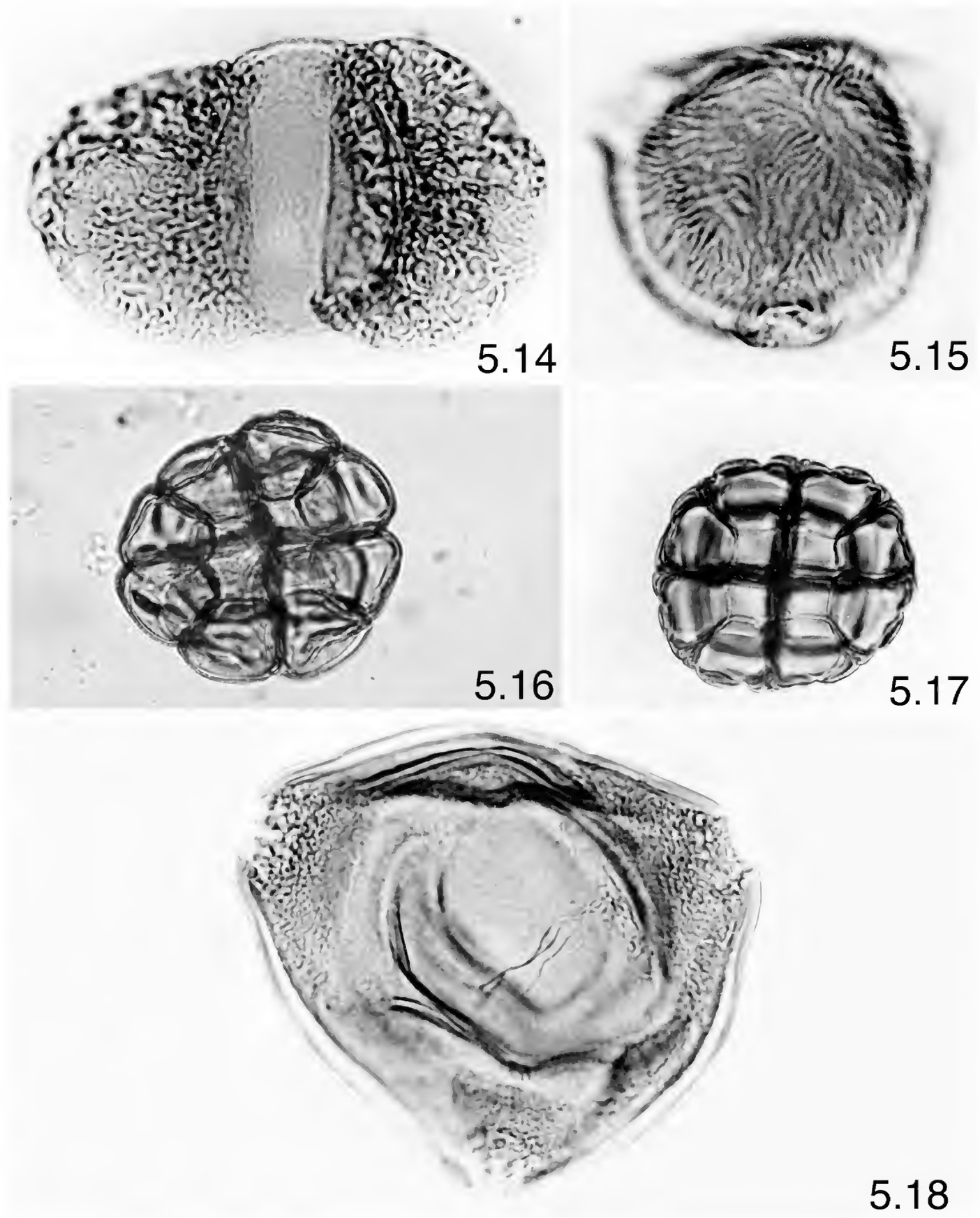


Figure 5.13. Plant megafossil fragments as illustrated from the middle Oligocene San Sebastián Formation of Puerto Rico. A, B. *Ficus* sp. C. *Sapindus*. D. *Melicocca* sp. E. *Icacorea* (?) sp. From Hollick (1928). Used with permission of Blackwell Publishing, Oxford, U.K.

just being defined within the transitional environments of the Oligocene (Figs. 5.2, 5.19). Furthermore, the landscape was restricted and much of proto-Puerto Rico was submerged (Chapter 2). Consequently, the vegetation as revealed by plant microfossils consists of only two communities. There was a mangrove formation (*Pelliceria*, *Rhizophora*) and a lower to upper montane broad-leaved forest distributed from just behind the coastal lagoons to moderate elevations in the central highlands (including the *Jamesonia–Eriosorus* complex; Sánchez-Baracaldo, 2004). The San Sebastián flora grew on the moist north-facing slope of these highlands. There is no evidence for desert, shrubland/chaparral–woodland–savanna, grassland, lowland Neotropical rain forest, coniferous forest, tundra, or alpine tundra (páramo) in the immediate vicinity. Areces-Mallea (1987) notes an unpublished and unconfirmed report by Cousminer (1957) of *Pinus* pollen in the Oligocene (undifferentiated) of Cuba. There were undoubtedly restricted beach/strand/dune, freshwater herbaceous bog/marsh/swamp, and aquatic communities. A few pollen grains in the San Sebastián flora were identified as *Fagus*, *Liquidambar*, and *Nyssa* (Graham & Jarzen, 1969),



Figures 5.14–5.18. Plant microfossils from the middle Oligocene San Sebastián Formation of Puerto Rico. 5.14. *Podocarpus*. 5.15. *Bursera*. 5.16. Modern pollen of *Acacia farnesiana*. 5.17. Fossil pollen of *Acacia* from the San Sebastián Formation. 5.18. *Hauya*.

and Hollick (1928) reported *Juglans* as a megafossil. Given the physiographic history of the Antilles as now understood and the overall record of northern temperate elements in the Latin American vegetation (Graham, 1999; Chapter 8), revision of the microfossil flora and confirmation of the megafossil identifications would be useful. The former study was published nearly 40 years ago, and the latter 80 years ago.

In Chapter 2, it was noted that a continuous or near-continuous strip of land called GAARlandia was proposed to connect northern South America to proto-Puerto Rico and the Virgin Islands across an emergent Aves Ridge (Iturralde-Vinent & MacPhee, 1999). It spanned the interval between ~32 and 29 Ma (Eocene–Oligocene transition) and was suggested, in part, to account for fossil remains of sloths in the Greater Antilles having South American affinities. Hedges (2001, 2006), who believes the region was occupied by islands, points out that some species of sloths swim in marine waters and that a continuous land bridge should have resulted in a greater number of terrestrial organisms common to the two regions. The paleobotanical evidence is equivocal, but the number of South American taxa (as listed by Raven & Axelrod, 1974) present in the older Paleogene of the Greater Antilles is not extensive (*Catostemma*, *Crudia*, *Eugenia–Myrcia*). By the middle Oligocene (San Sebastián flora), there were added *Podocarpus*, *Acacia*, *Aetanthus*, *Bombax*, *Brunelia*, *Casearia*, *Chrysophyllum*, *Corynostylis*, *Faramea*, *Guarea*, *Jacaranda*, *Marcgravia*, *Norantea*, *Pelliceria*, *Pleodendron*, *Rau(v)wolfia*, *Tecoma*, and *Tetrorchidium* (Graham, 2003b). Other means were available for introduction to the north (chance long-distance dispersal, movement through a fragmented proto-Antillean route), and the number of plants among those listed above requiring continuous land for migration is uncertain. The impression is that, like the faunal evidence, the presence of plants with South American affinities in the Paleogene of the Antilles would be greater if the Aves Ridge had been emergent and continuous land.

Table 5.1. Plant fossils from the Cretaceous and Cenozoic of the Antilles. Unless otherwise indicated, spellings, suggested biological affinities, and age assignments are according to the original authors. Unknowns and specimens designated by an informally applied artificial nomenclature are not included. Unpublished studies are cited in the References but are not included in the table. Spores and reproductive structures (e.g., cleistothecia) of fungi, Pyrrophyta (dinoflagellates), and diatoms and other algae are often treated in separate publications, and only those cited in the references below are included here. Refs. = references, as follows, Cretaceous: 1 = Smiley 1982, 2002, 2 = Areces-Mallea 1989, 3 = Habib 1969; Eocene: 4 = Areces-Mallea 1985, 5 = Areces-Mallea 1988, 6 = Areces-Mallea 1990, 7 = Graham et al. 2000, 7a = Graham 1993; Oligocene: 8 = Hollick 1928, 9 = Areces-Mallea 1987, 10 = Graham and Jarzen 1969; Miocene: 11 = Poinar and Singer 1990, 12 = Poinar and Thomas 1982, 13 = Stubblefield et al. 1985, 14 = Gómez 1982, 15 = Berry 1921, 16 = Berry 1923, 17 = Berry 1939, 18 = Dilcher et al. 1992, 19 = Cano and Borucki 1995, 20 = Graham 1990; Quaternary: 21 = Berry 1934, 22 = Iturralde-Vinent et al. 2000, 23 = Moncada Ferrera et al. 1990/91, 24 = Higuera-Gundy 1989.

Cretaceous [144–65 Ma; Early Cretaceous (Neocomian), 144–127 Ma, Middle Cretaceous (Aptian-Albian), 121–99 Ma]

Taxon	Flora/Formation	Age	Ref.
	Megafossils		
Ferns and allied groups			
Gleichenites	Los Ranchos, Dominican Republic	Neocomian	1
Gymnosperms			
Brachyphyllum	Los Ranchos	Neocomian	1
Frenelopsis	Los Ranchos	Neocomian	1
Phoenicopsis cf. *speciosa*	Los Ranchos	Neocomian	1
Podozamites cf. *eichwaldii*	Los Ranchos	Neocomian	1
Yuccites	Los Ranchos	Neocomian	1
Zamites cf. *buchianus*	Los Ranchos	Neocomian	1
Z. cf. *tenuinervis*	Los Ranchos	Neocomian	1
	Microfossils		
Ferns and allied groups			
Calamospora	Horizon A, Bahamas	Middle Cretaceous	3
Cicatricosisporites	Horizon A, Bahamas	Middle Cretaceous	3
C. crassiterminatus	San Adrián, Cuba	Middle Cretaceous	2
Concavisporites lamontis	Horizon A, Bahamas	Middle Cretaceous	3
Concavissimisporites punctatus	San Adrián, Cuba	Middle Cretaceous	2
Cyathidites australis	Horizon A, Bahamas	Middle Cretaceous	3
C. minor	Horizon A, Bahamas	Middle Cretaceous	3
Deltoidospora minor	San Adrián, Cuba	Middle Cretaceous	2
Dictyophyllidites	San Adrián, Cuba	Middle Cretaceous	2
Discisporites discoides	Horizon A, Bahamas	Middle Cretaceous	3
Gleicheniidites	Horizon A, Bahamas	Middle Cretaceous	3
G. apilobatus	Horizon A, Bahamas	Middle Cretaceous	3
G. circinidites	Horizon A, Bahamas	Middle Cretaceous	3
G. marciae	Horizon A, Bahamas	Middle Cretaceous	3
G. senonicus	Horizon A, Bahamas	Middle Cretaceous	3
	San Adrián, Cuba	Middle Cretaceous	2
G. severus	Horizon A, Bahamas	Middle Cretaceous	3
Laevigatosporites	Horizon A, Bahamas	Middle Cretaceous	3
L. ovatus	Horizon A, Bahamas	Middle Cretaceous	3
Lycopodiumsporites clavatoides	Horizon A, Bahamas	Middle Cretaceous	3
Microfoveolatosporis	San Adrián, Cuba	Middle Cretaceous	2
Muerrigerisporis (?) *sanadriensis*	San Adrián, Cuba	Middle Cretaceous	2
Stereisporites stereoides	San Adrián, Cuba	Middle Cretaceous	2
Taurocusporites reduncus	Horizon A, Bahamas	Middle Cretaceous	3
Todisporites minor	Horizon A, Bahamas	Middle Cretaceous	3
Gymnosperms—coniferous			
Alisporites bilateralis	Horizon A, Bahamas	Middle Cretaceous	3
Araucariacites australis	San Adrián, Cuba	Middle Cretaceous	2
A. limbatus	Horizon A, Bahamas	Middle Cretaceous	3
Parvisaccites majesticus	Horizon A, Bahamas	Middle Cretaceous	3
P. radiatus	Horizon A, Bahamas	Middle Cretaceous	3
Piceapollenites alatus	Horizon A, Bahamas	Middle Cretaceous	3
Platysaccus elizabethae	Horizon A, Bahamas	Middle Cretaceous	3
Pteruchipollenites crenulatus	Horizon A, Bahamas	Middle Cretaceous	3
P. transversus	Horizon A, Bahamas	Middle Cretaceous	2
Vitreisporites pallidus	Horizon A, Bahamas	Middle Cretaceous	3

Table 5.1. Plant fossils from the Cretaceous and Cenozoic of the Antilles. *(Continued)*

Taxon	Flora/Formation	Age	Ref.
Gymnosperms—Cycadalean			
Cycadopites	San Adrián, Cuba	Middle Cretaceous	2
Eucommiidites	Horizon A, Bahamas	Middle Cretaceous	3
E. cf. *troedsonii*	San Adrián, Cuba	Middle Cretaceous	2
Inaperturopollenites dubius	Horizon A, Bahamas	Middle Cretaceous	3
cf. *I. hiatus*	San Adrián, Cuba	Middle Cretaceous	2
	Horizon A, Bahamas	Middle Cretaceous	3
I. aff. *scabratus*	San Adrián, Cuba	Middle Cretaceous	2
Monosulcites chaloneri	Horizon A, Bahamas	Middle Cretaceous	3
M. inspissatus	Horizon A, Bahamas	Middle Cretaceous	3
M. minimus	Horizon A, Bahamas	Middle Cretaceous	3
Spheripollenites psilatus?	Horizon A, Bahamas	Middle Cretaceous	3
Zonalapollenites dampieri	Horizon A, Bahamas	Middle Cretaceous	3
Angiosperms—monocotyledonous			
Liliacidites dividuus	Horizon A, Bahamas	Middle Cretaceous	3
Monosulcites	San Adrián, Cuba	Middle Cretaceous	2
Angiosperms—dicotyledonous			
Circulina parva	San Adrián, Cuba	Middle Cretaceous	2
Quercus aurita [?, Fagaceae]	Horizon A, Bahamas	Middle Cretaceous	3
Retitricolpites georgensis	Horizon A, Bahamas	Middle Cretaceous	3
R. sphaeroides	Horizon A, Bahamas	Middle Cretaceous	3
R. vulgaris	San Adrián, Cuba	Middle Cretaceous	2
R. sp.	San Adrián, Cuba	Middle Cretaceous	2
Tricolpollenites minutus	Horizon A, Bahamas	Middle Cretaceous	3
T. polyhedrus	Horizon A, Bahamas	Middle Cretaceous	3
Incertae sedis			
Clavatipollenites hughesii	Horizon A, Bahamas	Middle Cretaceous	3
C. maximus	Horizon A, Bahamas	Middle Cretaceous	3
Galeacornea	Horizon A, Bahamas	Middle Cretaceous	3
Palynomorph type A	Horizon A, Bahamas	Middle Cretaceous	3
Schizosporis burcklei	Horizon A, Bahamas	Middle Cretaceous	3
Acritarchs			
Diplotesta inflata	Horizon A, Bahamas	Middle Cretaceous	3
Palaeostomocystis fragilis	Horizon A, Bahamas	Middle Cretaceous	3
Prismatocystis ewingii	Horizon A, Bahamas	Middle Cretaceous	3
Hystrichosphaerids			
Hystrichosphaeridium	Horizon A, Bahamas	Middle Cretaceous	3
H. arundum	Horizon A, Bahamas	Middle Cretaceous	3
Dinoflagellates			
Canningia minor	Horizon A, Bahamas	Middle Cretaceous	3
Scriniodinium	Horizon A, Bahamas	Middle Cretaceous	3
Stephodinium cf. *europaicum*	Horizon A, Bahamas	Middle Cretaceous	3

Eocene (54.8–33.7 Ma)

Microfossils

[4, Saramaguacán Formation, middle Eocene, Province Camagüey, Cuba]

Angiosperms (dicotyledons): *Bombacacidites mirabilis* [Bombacaceae–Sterculiaceae–Tiliaceae]

[5, Saramaguacán Formation, middle Eocene, Province Camagüey, Cuba]

Ferns and allied groups: *Concavisporites* cf. *stavensis*, *Laevigatosporites haardtii*, *Lygodiumsporites adriennis*, *Ornatisporites* aff. *dentatus*, *Polypodiisporonites alienus*, *P.* cf. *favus*. Angiosperms (monocotyledons): *Arecipites columellus*, *A. punctatus* (Palmae), *Graminidites gramineoides* (Gramineae), *Liliacidites intermedius*, *Monocolpopollenites* aff. *tranquillus*

[6, Saramaguacán Formation, middle Eocene, Province Camagüey, Cuba]

Basopollis krutz(s)chi [normapolles]

[7, Saramaguacán Formation, middle Eocene, Province Camagüey, Cuba]

Ferns and allied groups: *Laevigatosporites*, *Lygodiumsporites adriennis*, cf. *Pteris dentata* (Pteridaceae), Trilete fern spore type 1, *Undulatisporites concavus*, *Verrucatosporites usmensis*. Angiosperms (monocotyledons): *Arecipites* (Palmae), *Graminidites gramineoides* (Gramineae), *Liliacidites*, *Retimonocolpites* types 1–5. Angiosperms (dicotyledons): *Basopollis–Brosipollis* cf. *striata–Choanopollenites* [normapolles group, possibly aff. Juglandaceae], *Bombacacidites* cf. *tilioides*, *B.* types 1, 2 [Bombacaceae–Sterculiaceae–Tiliaceae], *Cupuliferoidaepollenites liblarensis*, *Echitricolpites*, *Fraxinopollenites* cf. *scoticus*, *Lymingtonia* cf. *rhetor*, *Malvacipollis tschudyi*, *Myrtaceidites* cf. *parvus*, *Pericolporites*, *Porocolpopollenites*, *Psilodiporites redundantis*, *Retibrevitricolpites*, *Retibrevitricolporites*, *Reticulataepollis* cf. *intergranulata*, *Retipollenites* cf. *confusus*, *Retitricolpites* types 1–6, *Retitricolporoides* types 1–3, *Striatricolpites catatumbus* (cf. *Crudia*, Leguminosae), *Triporopollenites* types 1, 2

[7a, Guys Hill Formation, middle Eocene, Trelawny Parish, Jamaica]

Ferns and allied groups: *Deltoidospora* (cf. *D. adriennis*). Angiosperms (monocotyledons): *Mauritidites*, *Retimonocolpites* (Palmae). Angiosperms (dicotyledons): *Bombacacidites* (Bombacaceae), *Corsinipollenites* (Onagraceae), *Cupaneidites* (Sapindaceae), *Psilatricolporites crassus* (*Pelliceria*, Pelliceriaceae)

Table 5.1. Plant fossils from the Cretaceous and Cenozoic of the Antilles. *(Continued)*

Oligocene (33.7–23.8; middle Oligocene ~31–22 Ma)

Megafossils

[8, San Sebastián Formation, middle Oligocene, Quebrada Collazo, Lares–San Sebastián, Puerto Rico]

Algae: *Chondrites dictyotoides*. Ferns and allied groups: *Hemitelia* [*Cnemidaria*] *brannerii* (Cyatheaceae), *Isoëtes* (?) *incerta* (Isöetaceae). Gymnosperms: *Zamia collazoënsis*, *Z. noblei* (Cycadaceae). Angiosperms (monocotyledons): *Bactris pseudocuesco* (Palmae), *Iriartea collazoënsis* (Palmae), *Manicaria portoricensis* (Palmae), *Musophyllum* (Musaceae), *Palmacites alius*, *P. conformis*, *P. sparsistriatus* (Palmae), *Palmocarpon acrocomioides*, *P. cetera*, *P. exemplare*, *P. opinabile*, *P. rabellii* (Palmae), *Palmophyllum* (Palmae). Angiosperms (dicotyledons): *Acrodiclidium pseudocanelo*, *A. pseudosalicifolium* (Lauraceae), *Aniba collazoensis* (Lauraceae), *Annona cetera*, *A. pseudoglabra* (Annonaceae), *Apocynophyllum pseudowillughbya*, *A. wilcoxense* (?) (Apocynaceae), *Aspidosperma collazoënsis* (Apocynaceae), *Cassia* (?) *dubiosa*, *C. evidens*, *C. imitativa*, *C. imparilis*, *C. ordinaria*, *C. puryearensis*, *C. visibilis* (Leguminosae), *Chrysophyllum comparabile*, *C. pseudargenteum*, *C. pseudargenteum* var. *oblongum* (Sapotaceae), *Combretum pseudojacquinii* (Combretaceae), *Copaiva* [*Copaifera*] *oligocenica* (Leguminosae), *Cynometra rabellii* (Leguminosae), *Dipholis pseudoleiantha* (Sapotaceae), *Echites pseudostellaris* (Apocynaceae), *Eugenia comparabilis*, *E. pseudaeruginea* (Myrtaceae), *Ficus hyphodroma*, *F. schimperi*, *F. vexativus*, *F.* sp. (Moraceae), *Guarea opinabilis* (Meliaceae), *Guettarda intercalaris* (Rubiaceae), *Hancornia minor*, *H. pseudopubescens* (Apocynaceae), *Hufelandia portoricensis* (Lauraceae), *Icacorea prisca*, *I.* (?) sp. (Myrsinaceae), *Inga curta*, *I. pseudinsignis*, *I. pseudonobilis*, *I. pseudospuria*, *I.* sp. (Leguminosae), *Lonchocarpus praelatifolius* (Leguminosae), *Malvocarpon clarum* (Malvaceae), *Melicoccus immutata*, *M.* sp. (Sapindaceae), *Misanteca dubiosa* (Lauraceae), *Myrcia denuntiativa* (Myrtaceae), *M. eugenioides*, *Myrsine pseudoferruginea* (Myrsinaceae), *Oreodaphne mississippiensis* (Lauraceae), *Pithecellobium* (?) *imperfectum*, *P. pseudotrapezifolium*, *P. vexativum* (Leguminosae), *Plumiera evidens* (Apocynaceae), *Psidium dissimile*, *P.* sp. (Myrtaceae), *Rhizophora* (?) *doctrinalis* (Rhizophoraceae), *Sapindus brittonii*, *S. gracilentus*, *S. obesus*, *S. pseudomarginatus* (Sapindaceae), *Sapota agnitionalis* (Sapotaceae), *Sideroxylon aequale* (Sapotaceae), *Sophora* (?) *suspecta* (Leguminosae), *Stylogyne* (?) *fragmenta* (Myrsinaceae), *Trichilia evidens*, *T. pseudobakerii*, *T. pseudohirta*, *T. spatulata* (Meliaceae), *Zizyphus pseudochloroxylon* (Rhamnaceae). Incertae sedis: *Echitonium* (?), *Ramulus* gen. et sp. (?)

Microfossils

[9, Oligocene, Punta Alegre Well, Province Ciego de Ávila, Cuba]

Gymnosperms: *Pinus* (aff. *P. tropicalis*; Pinaceae)

[10, San Sebastián Formation, middle Oligocene, Quebrada Collazo, Lares–San Sebastián, Puerto Rico]

Ferns and allied groups: *Lycopodium* (types a, b; Lycopodiaceae), *Selaginella* (Selaginellaceae), *Cyathea* (Cyatheaceae), *Cnemidaria* (*Hemitelia*; Cyatheaceae), *Jamesonia–Eriosorus* (Pteridaceae), *Pteris* (types a, b, c; Pteridaceae), monolete fern spores, trilete fern spores. Gymnosperms: *Podocarpus* (Podocarpaceae). Angiosperms (dicotyledons): *Abutilon* (Malvaceae), *Acacia* (Leguminosae), *Aetanthus* (Leguminosae), *Alchornea* (Euphorbiaceae), *Bernoullia* (Bombacaceae), *Bombax* [now Bombacaceae; *Bombax* is treated as an African genus], *Brunellia* (Brunelliaceae), *Bursera* (Burseraceae), *Casearia* (Flacourtiaceae), *Catostemma* (Bombacaceae), *Chrysophyllum* (Sapotaceae), *Corynostylis* (Violaceae), *Dendropanax* (Araliaceae), *Engelhard(t)ia* [now *Alfaroa–Oreomunnea*; *Engelhardia* is treated as an Asian genus; Juglandaceae], *Eugenia* (now *Eugenia–Myrcia*; Myrtaceae), *Fagus* [?; Fagaceae], *Faramea* (Rubiaceae), *Guarea* (Meliaceae), *Hauya* (Onagraceae), *Ilex* (Aquifoliaceae), *Jacaranda* (Bignoniaceae), *Liquidambar* [?; Hamamelidaceae], *Marcgravia* (Marcgraviaceae), *Myrcia* [as *Myrica*; Myrtaceae], *Norantea* (Marcgraviaceae), *Nyssa* [?; Nyssaceae], *Oxalis* (Oxalidaceae), *Pelliceria* (Pelliceriaceae), *Pleodendron* (Canellaceae), *Rau(v)wolfia* (Apocynaceae), *Rhizophora* (Rhizophoraceae), *Salix* (Salicaceae), *Tecoma* (Bignoniaceae), *Tetrorchidium* (Euphorbiaceae), *Tournefortia* (Boraginaceae), *Zanthoxylum* (Rutaceae)

Miocene (23.8–5.3 Ma; including Late Tertiary undifferentiated; amber fossils included under Oligocene–Miocene amber; for amber material of bryophytes *Baccania*, *Drepanolejeunia*, *Frullania*, and *Octoblepharum*, and the legume *Hymenaea*; see text)

Megafossils

[11, La Toca mine, El Mamey Formation, Miocene, Santiago–Puerto Plata, Cordillera Septentrional, amber, Dominican Republic]

Fungi: *Coprinites dominicana* (Coprinaceae, Basidiomycetes, gilled mushroom)

[12, formation/location unspecified, Miocene, entomophthorelean fungus, probably *Entomophthora*, amber, Dominican Republic]

[13, formation/location unspecified, Miocene, amber, Dominican Republic]

Fungi: *Geotrichites glaesarius* (resembles *Geotrichium candidum*, moniliaceous member of Deuteromycotina)

[14, formation/location unspecified, Miocene, amber, Dominican Republic]

Ferns and allied groups: *Grammitis succinea* (Polypodiaceae). Angiosperms (monocotyledons): *Trithrinax dominicana* (Palmae; Poinar, 2002)

[15, miscellaneous assemblage from five localities, most near pier at Sánchez, north coast of Dominican Republic, Late Tertiary; under Oligocene, Oligo–Miocene Appendix 2.1]

Angiosperm (monocotyledon): *Poacites* (Gramineae). Angiosperms (dicotyledons): *Bucida sanchezensis* (Combretaceae), *Bumelia reclinatafolia* (Sapotaceae), *Calyptranthes domingensis* (Myrtaceae), *Guettardia cookei* (Rubiaceae), *Inga sanchezensis*, *I.* sp. (Leguminosae), *Melastomites domingensis*, *M.* sp. (Melastomataceae), *Pisonia conditi* (Nyctaginaceae), *Pithecolobium samanensis* (Leguminosae), *Sapindus hispaniolana* (Sapindaceae), *Sophora cookei* (Leguminosae)

[16, miscellaneous assemblage from 13 localities, most yielding undeterminable fragments, most from Département de l'Ouest, cut along road from Mirebalais to Las Cahobas, Miocene, Haiti; under Oligo–Miocene Appendix 2.1]

Algae: *Chara woodringi*. Ferns and allied groups: *Gymnogramme(a)* (*Hemionitis*) *woodringi* (now distributed among several genera; Pteridaceae). Angiosperms (dicotyledons): *Bumelia cuneatafolia* (Sapotaceae), *Chrysophyllum cahobasensis* (Sapotaceae), *Guettarda cookei* (Rubiaceae), *Mespilodaphne hispaniolana* (Lauraceae), *Mimusops praeparvifolia* (Sapotaceae), *Pisonia conditi* (Nyctaginaceae), *Simaruba haitensis* (Simarubaceae)

[17, Yumurí Gorge, Miocene (Oligo–Miocene Appendix 2.1), Matanzas Province, Cuba]

Ferns and allied groups: *Gleichenia pectinataformia* (*-forma* in systematic list; Gleicheniaceae). Angiosperms (monocotyledons): *Heliconia* (Heliconiaceae), palm rays. Angiosperms (dicotyledons): *Bignonia zuliana* (Bignoniaceae), *Bumelia retusafolia* (Sapotaceae), *Caesalpinia prebahamensis* (Leguminosae), *Caesalpinites incertus* (Leguminosae),

Table 5.1. Plant fossils from the Cretaceous and Cenozoic of the Antilles. *(Continued)*

Calophyllum calabaformis (Guttiferae), *Capparis prejamaicensis* (Capparidaceae), *Cassia yumuriensis* (Leguminosae), *Celastrus simplex* (Celastraceae), *Dalbergia hesperia* (Leguminosae), *Dodonaea cubensis* (Sapindaceae), *Drypetes laterifloraforma* (Euphorbiaceae), *Eugenia ovatifolia* (Myrtaceae), *Exostema precaribaeum* (Rubiaceae), *Fagara miocenica* (Rutaceae), *Inga leonii*, *I. miocenica* (Leguminosae), *Laguncularia racemosafolia* (Combretaceae), *Metopium prenuntium* (Anacardiaceae), *Mimusops leonii*, *M. miocenica* (Sapotaceae), *Myrcia minor*, *M. prerostrata* (Myrtaceae), *Pisonia longifoliaformis* (Nyctaginaceae), *Pithecolobium yumuriensis* (Leguminosae), *Pseudolmedia spuriaformis* (Moraceae), *Reynosia latifolioides* (Rhamnaceae), *Rheedia silvargillacea* (Guttiferae), *Sapindus presaponaria* (Sapindaceae), *Simaruba glaucaformis* (Simarubaceae), *Sophora maranoides*, *S. matanzana*, *S. yumuriensis* (Leguminosae), *Swietenia mahagoniformis* (Meliaceae), *Trichilia hirtaformis* (Meliaceae), *Zizyphus elliptica*, *Z. minor* (Rhamnaceae). Incertae sedis: *Antholithus heimiaformis*

[18, Palo Alto Mine, Altimira Formation, Miocene, Cordillera Septentrional, Dominican Republic]

Angiosperm (dicotyledons): *Acacia eocaribbeanensis* (Leguminosae)

Microfossils

[19, locality unspecified, Miocene, Dominican Republic]

Bacteria: *Bacillus* [revived, cultured, and identified fide authors (19)]

[20, Artibonite Group, Miocene, north of the Cul-de-Sac/Enriquillo Basin, Départemente de l'Ouest, cut along road from Mirebalais to Las Cahobas, Haiti]

Ferns and allied groups: *Alsophila* (Cyatheaceae), *Pteris* (types 1–3; Pteridaceae), cf. *Antrophyum* (Vittariaceae), monolete fern spore, trilete fern spores types 1, 2. Gymnosperm: *Pinus* (Pinaceae). Angiosperm (monocotyledons): Palmae types 1, 2. Angiosperms (dicotyledons): *Alchornea* (Euphorbiaceae), *Alfaroa–Oreomunnea* (Juglandaceae), *Allophylus* (Sapindaceae), chenoams, Compositae types 1–4, *Hygrophila* (Acanthaceae), Malpighiaceae, *Oryctanthus* (Loranthaceae)

Quaternary (~2.6 Ma to present)

Megafossils

[21, Chapapote Hot Springs, Santa Clara Province; Sabanilla de las Palmas, Matanzas Province; Pleistocene, Cuba]

Gymnosperm: *Juniperus* (Cupressaceae), *Pinus caribaea* (Pinaceae). Angiosperms (dicotyledons): *Chrysobalanus icaco* (Chrysobalanaceae), *Conocarpus* (Combretaceae), *Mimusops emarginata* (Sapotaceae), *Spondias lutea* (Anacardiaceae)

[22, Las Breas de San Felipe, Matanzas Province, Pleistocene–Holocene, Cuba]

Gymnosperms: *Pinus caribaea* (Pinaceae). Angiosperms (monocotyledons): *Coccothrinax* (Palmae), *Thrinax radiata* (Palmae). Angiosperms (dicotyledons): *Calophyllum* (Guttiferae), *Chrysobalanus icaco* (Chrysobalanaceae), *Cordia galeottiana*, *C. sesbestena* (Boraginaceae), *Ficus* (Moraceae), *Spondias lutea* (Anacardiaceae)

Microfossils

[23, Isla de la Juventud (cores just off western end of island), Pleistocene, Cuba; some identifications are to species because of the recent age of the sediments]

Algae: *Botryococcus*, Hystrichosphaera. Ferns and allied groups: *Acrostichum aureum* (Pteridaceae), cf. *Anemia* (Schizaeaceae), *Blechnum*, *B. serrulatum* (Blechnaceae), *Lygodium* (Schizaeaceae), *Polypodium* (Polypodiaceae), *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae), tipo trilete. Gymnosperms: *Pinus caribaea*, *P. tropicalis* (Pinaceae), *Podocarpus angustifolius* (Podocarpaceae). Angiosperms (monocotyledons): *Acoelorraphe wrightii* (Palmae), *Acrocomia* (Palmae), Bromeliaceae, *Cladium jamaicense* (Cyperaceae), *Colpothrinax wrightii* (Palmae), Cyperaceae, *Cyperus* (Cyperaceae), Gramineae, Palmae, *Sabal parviflora* (Palmae), *Typha*, *T. domingensis* (Typhaceae). Angiosperms (dicotyledons): *Allophylus* (Sapindaceae), *Amaranthus* (Amaranthaceae), *Amaranthus*/Chenopodiaceae, *Ambrosia* (Compositae), Anacardiaceae, tipo *Bombax* (Bombacaceae), *Borreria* (Rubiaceae), *Bucida–Conocarpus* (Combretaceae), *Bunchosia* (Malpighiaceae), *Bursera simaruba* (Burseraceae), *Caperonia palustris* (Euphorbiaceae), *Casearia* (Flacourtiaceae), *Catostemma* (?) (Bombacaceae), Chenopodiaceae, *Cissus* (Vitaceae), *Corchorus* (Tiliaceae), *Cuphea* (Lythraceae), *Cyrilla racemiflora* (Cyrillaceae), *Daphnopsis* (Thymelaeaceae), *Eichornia crassipes* (Pontederiaceae), Ericaceae, *Evolvulus* (Convolvulaceae), *Faramea occidentalis* (Rubiaceae), *Ficus* (Moraceae), *Gouania* (Rhamnaceae), *Guettarda calyptrata* (Rubiaceae), *Heliotropium* (Boraginaceae), *Ilex* (Aquifoliaceae), *Ipomoea* (Convolvulaceae), *Jacaranda coerulea* (Bignoniaceae), Labiatae, Malpighiaceae, Malvaceae, Melastomataceae, Meliaceae, *Metopium* (Anacardiaceae), Moraceae, *Myrica cerifera* (Myricaceae), Myrtaceae, *Nymphaea* (Nymphaeaceae), *Nymphoides grayana* (Menyanthaceae), Onagraceae, *Picrodendron macrocarpum* (Picrodendraceae), *Protium cubense* (Burseraceae), *Rau(v)wolfia* (Apocynaceae), *Rhizophora mangle* (Rhizophoraceae), Sapotaceae, *Spondias* (Anacardiaceae), *Trema* (Ulmaceae), *Tribulus* (Zygophyllaceae), Umbelliferae (Apiaceae), *Utricularia* (Lentibulariaceae), *Xylopia aromatica* (Annonaceae)

[24, Lake Miragoane, Haiti, Holocene (Recent)]

Gymnosperm: *Pinus* (Pinaceae). Angiosperms (monocotyledons): *Cladium* (Cyperaceae), Cyperaceae, Gramineae, *Typha* (Typhaceae), *Zea mays* (Gramineae). Angiosperms (dicotyledons): *Alchornea* (Euphorbiaceae), *Ambrosia* (Compositae), *Bursera* (Burseraceae), *Caesalpinia* (Leguminosae), *Cecropia* (Urticaceae), *Celtis* (Ulmaceae), chenoams, Compositae, Euphorbiaceae, Melastomataceae, Meliaceae (probably *Swietenia*), Myrtaceae, *Nelumbo* (Nymphaeaceae), *Nymphaea* (Nymphaeaceae), *Phyllostylon* (Ulmaceae), *Pilea* (Urticaceae), *Potamogeton* (Potamogetonaceae), *Sapindus* (Sapindaceae), Sapotaceae, Solanaceae, *Trema* (Ulmaceae)

MIOCENE (23.8–5.3 MA)

Amber in the Greater Antilles: Amber is known from the Maastrichtian–Paleocene of Jamaica, in Oligocene and Miocene lignites of Puerto Rico (Iturralde-Vinent & Hartstein, 1998), and in Miocene lignites of Cuba, Haiti, and the Dominican Republic. The varied terminology used for amber and related sediments is defined as follows (Iturralde-Vinent, 2001):

Resin—recently extruded from the tree,

Copal—older deposits found in the leaf litter or buried soil,

Amber—fossilized resin often buried deeply in older sedimentary strata, and

Resinite—general term for all plant-derived resins.

The amber deposits of the Dominican Republic contain biological inclusions and were deposited during the late early Miocene to early middle Miocene (15–20 Ma; Iturralde-Vinent,

2001; Iturralde-Vinent & MacPhee, 1996). They come primarily from two sites, north of Santiago de Los Caballeros (19°N, 70°W; La Toca Formation) and northeast of Santo Domingo (18°N, 69°W; Yanigua Formation; Fig. 5.20), although the source of some purchased specimens in various collections is unknown. Among the inclusions are bacterial spores from the abdominal contents of an extinct species of bee (*Proplebeia dominica*). These purportedly were revived, cultured, and identified as *Bacillus* fide Cano and Borucki (1995; see Brodie, 2005). Also present in Antillean amber are the fungi *Geotrichites glaesarius* from the surface of a fossilized arachnid (Stubblefield et al., 1985; Fig. 5.21), an entomophthoraceous phycomycete (probably *Entomophthora*; Poinar & Thomas, 1982), and *Coprinites dominicana* (Poinar & Singer, 1990; Fig. 5.22); the bryophytes *Bazzania*, *Drepanolejeunia*, *Frullania*, and *Octoblepharum* (Hueber & Langenheim, 1986); the fern *Grammitis succinea* (Gómez, 1982); flowers of *Trithrinax dominicana* (Arecaceae; Poinar, 2002); a flower of *Acacia* (Dilcher et al., 1992; Fig. 5.23); and leaf fragments, wood, and flowers of *Hymenaea*. Although *H. courbaril* is the only species of the genus that presently grows on the island, the morphology of the flowers (tufts of hairs at the base of the ovary) and infrared spectrophotometry of the resin shows closest affinities with *H. verrucosa* of the dry lowland evergreen forest and semi-deciduous lowland forest of east-coastal tropical Africa and adjacent islands (Hueber & Langenheim, 1986).

Amber has a potentially valuable but debated use in paleoclimatic reconstructions. It contains bubbles of air trapped as the resin is being produced, and mass spectrometry can be used to identify and estimate the percentage of the components (Berner & Landis, 1988). A survey of Late Cretaceous to Miocene amber, including material from the Dominican Republic, showed a decline in oxygen concentration from >30% to 21%. Although the composition of atmospheric gases from air bubbles has been calculated for Quaternary ice, knowing the changing concentrations of greenhouse gases such as CO_2 and methane from older sediments and from an independent source would be valuable. Unfortunately, it is likely that atmospheric molecules diffuse through amber, and that it does not faithfully preserve ancient air over geologic time [see Technical Comments, *Science* 241 (1988): 717–724].

Megafossils are known from the Miocene Artibonite flora of Haiti at a locality along the road from Mirebalais to Las Cahobas just north of the Cul-de-Sac/Enriquillo Basin in the Département de l'Ouest (Berry, 1923; Fig. 5.24). The geologic formations at the site are the Madame Joie, Maissade, and Thomonde (Iturralde-Vinent & MacPhee, 1999; Bowin, 1975 includes Las Cahobas; Fig. 5.25). The position of the plant-bearing beds within these formations is not specified, but all are within the Miocene and probably 5–7 Ma old. Pieces of the matrix from Berry's specimens were processed for microfossils, and a small assemblage of 25 fossil spores and pollen was recovered (Graham, 1990; Figs. 5.26–5.28). There were no dinoflagellates, or pollen of *Pelliceria* or *Rhizophora*, indicating deposition in an inland marsh beyond marine inundation. Pollen of *Pinus* was abundant (16%), but there are no intervening records between its possible presence in the Oligocene of Cuba and its documented presence in the Mio–Pliocene of Haiti to fix its earliest appearance in the Antilles. The principal paleocommunities of the Artibonite flora were a lower to upper montane broad-leaved forest formation with a cloud forest association, a coniferous forest surrounding a freshwater herbaceous bog/marsh/swamp with abundant ferns (*Laevigatisporites*, 36%), and an aquatic community (*Hygrophila*).

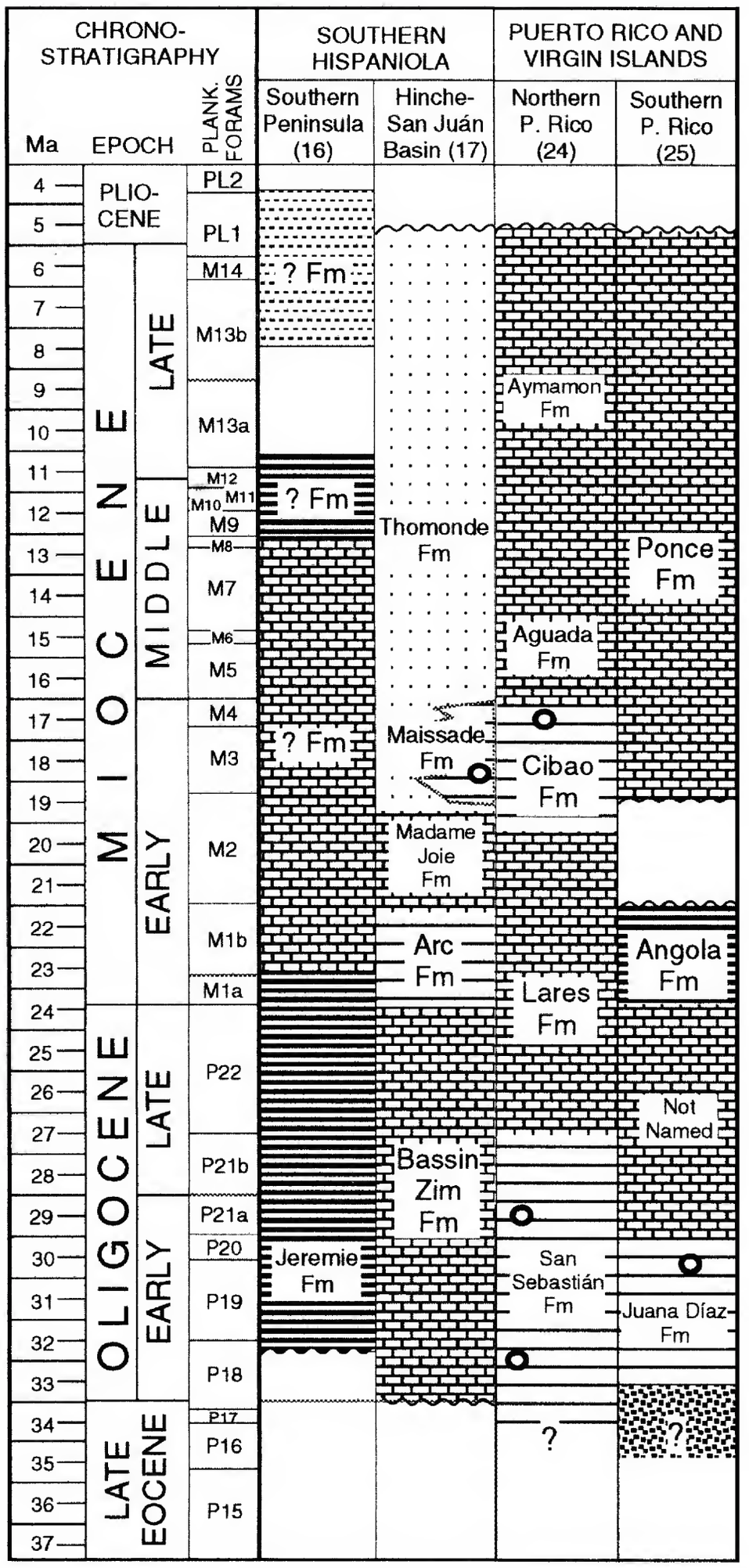


Figure 5.19. Stratigraphic columns for selected basins of the Greater Antilles. From Iturralde-Vinent and MacPhee (1999). Courtesy of the American Museum of Natural History.

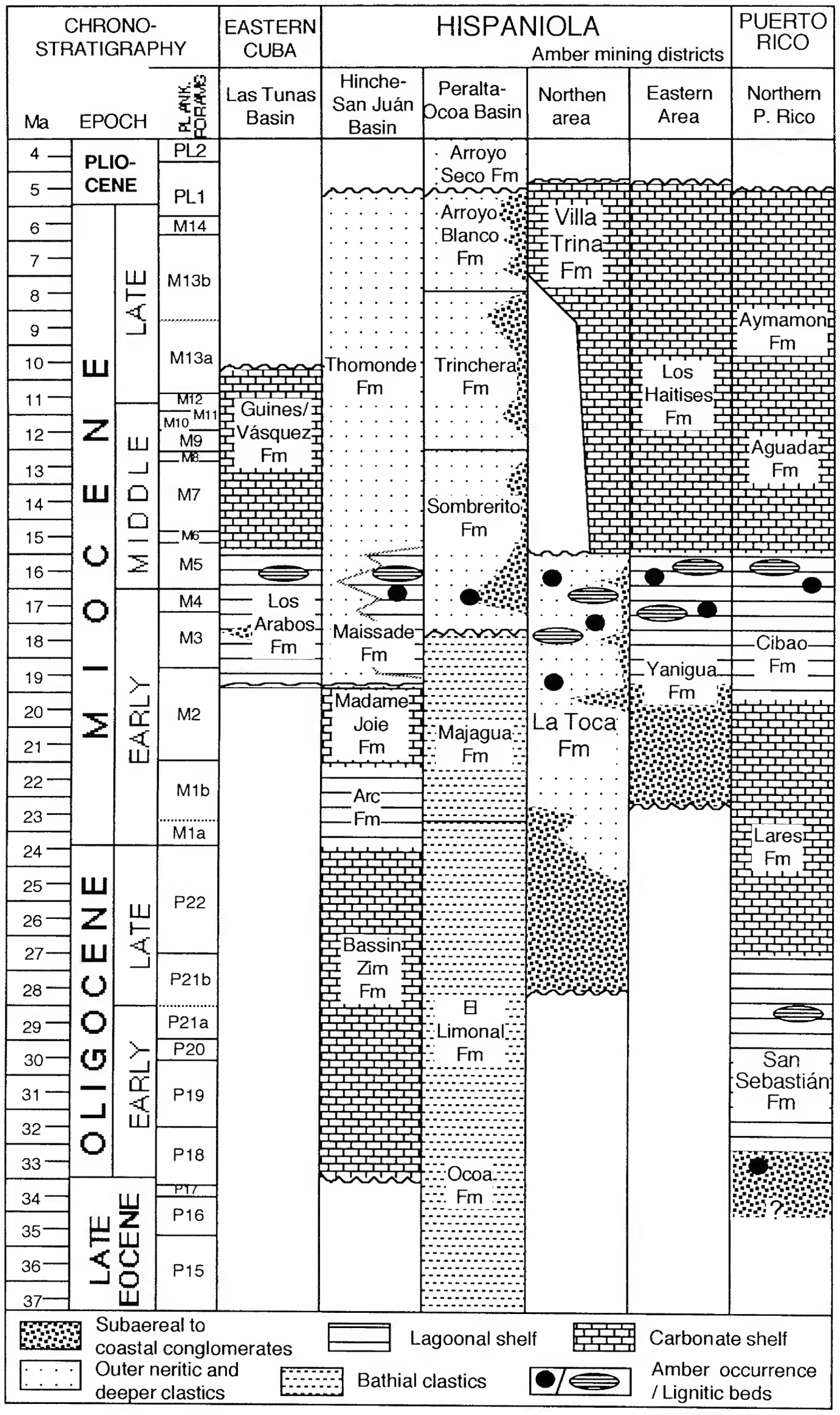


Figure 5.20. Oligocene and Miocene formations of the Greater Antilles. From Iturralde-Vinent (2001). Used with permission of the *Caribbean Journal of Science*.

The relatively young age of the flora and the detailed inventory available for the modern cloud forest and coniferous forest communities (Chapter 3) allow a close estimate of the paleoelevation. It extended from sea level to ~1400 m near the site (the present highest elevation is ~2680 m on Morne de la Selle in the southeastern part of the country). The MAT was probably 23°–26° C at 400 m elevation and 17°–19° C at 1400 m. The affinities of the fossil flora are with North America, and the one element not present in the modern vegetation of Haiti (*Alfaroa–Oreomunnea*) occurs in adjacent Mexico and Central

Figure 5.21. Hyphae and chains of conidia of *Geotrichites glaesarius* from the Dominican amber. From Stubblefield et al. (1985). Reprinted by permission from the New York Botanical Garden, Bronx, and Thomas N. Taylor.

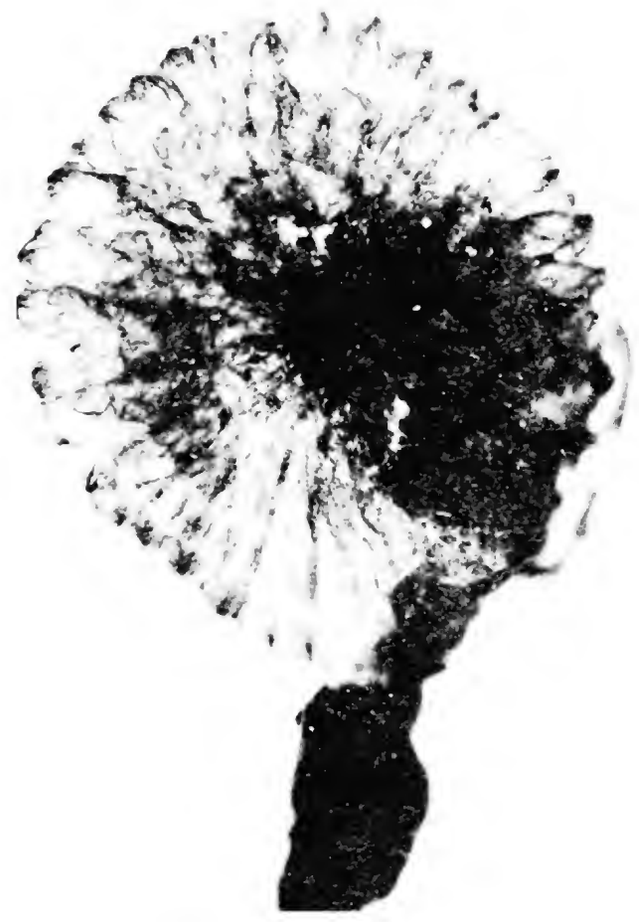


Figure 5.22. Pilus of *Coprinites dominicana* from the Dominican Republic. From Poinar and Singer (1990). Used with permission of *Science*.

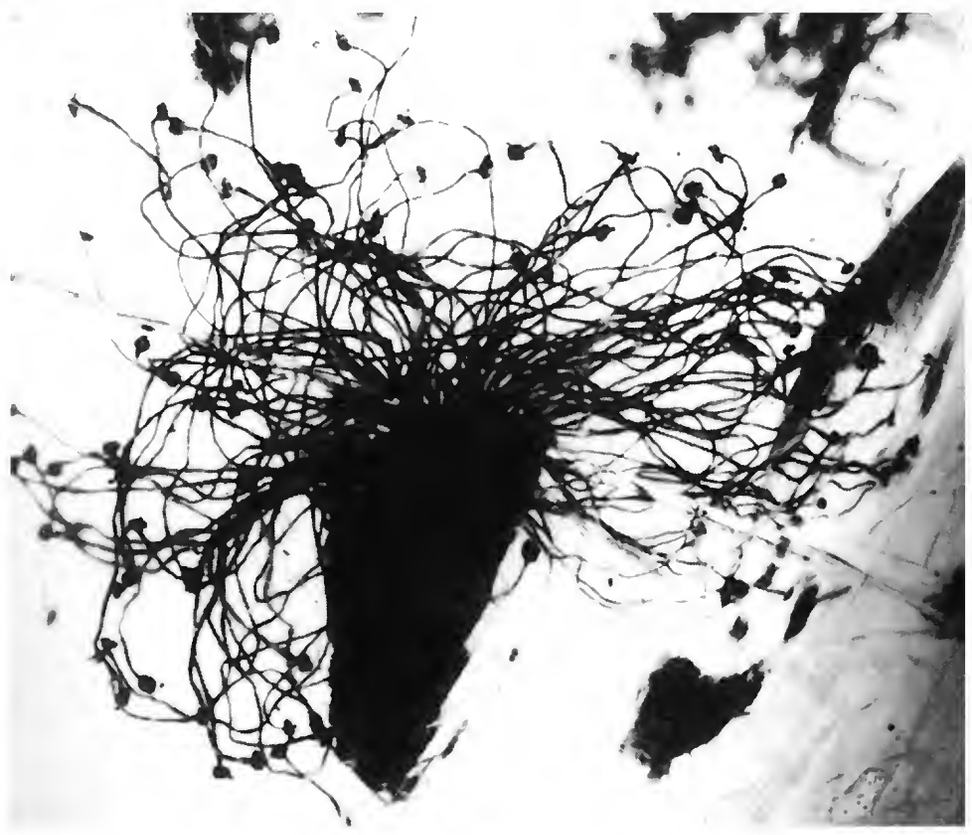


Figure 5.23. Fossil flower of *Acacia eocaribbeanensis* from the Dominican amber. From Dilcher et al. (1992). Copyright The Board of Trustees of the Royal Botanic Gardens, Kew.

America. The only other estimate of terrestrial MAT based on paleobotanical evidence is ~26° C for the middle Oligocene San Sebastián flora of Puerto Rico (Graham & Jarzen, 1969), and both are broadly consistent with the Neogene cooling trend evident on the paleotemperature curve (Fig. 5.2).

There are other Neogene floras in the Antilles of uncertain age but probably belonging to the Miocene (Tertiary undifferentiated in Table 5.1). One is from the Yumurí River Valley, Matanzas Province, Cuba (Berry, 1939; Table 5.1; Figs. 5.29A–D). Thirty-eight species that likely represent a lowland flora inland from the coast are described. There is one specimen of *Laguncularia* and none of *Rhizophora*, but the sediments have not been examined for the presence of marine dinoflagellates or other plant microfossils. The leaves are mostly small and entire margined, but the old procedure of outlining leaf margins with ink (Fig. 5.29A) requires reexamination of the

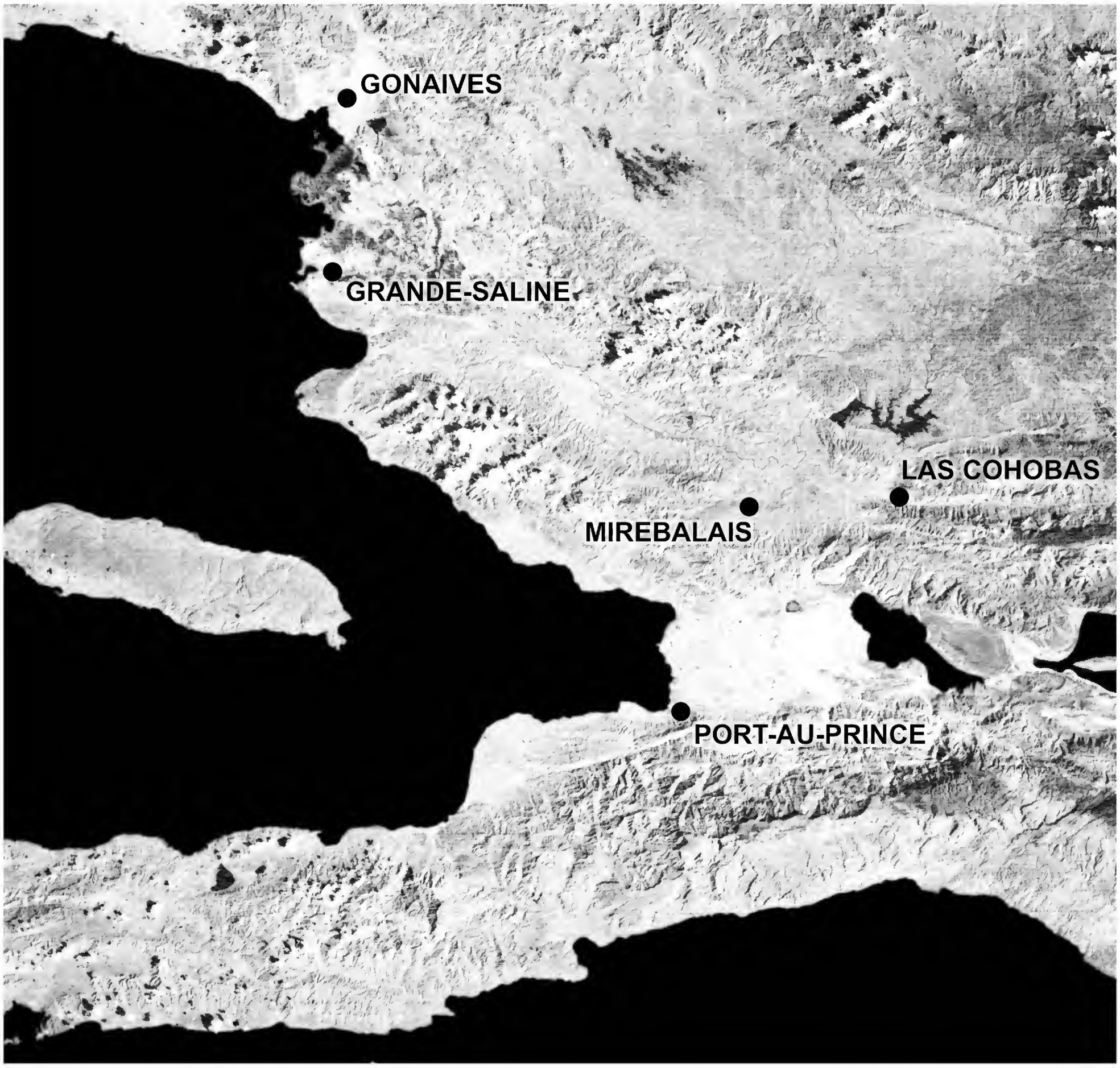


Figure 5.24. Cul-de-Sac/Enriquillo Basin region of Haiti. From Maurrasse (1982). Satellite image by NASA Johnson Space Center, Earth Sciences & Image Analysis.

specimens for purposes of LMA.

In the Dominican Republic, there are megafossils of Late Tertiary to possibly Pleistocene age known from several sites, but principally from near the pier at Sánchez on the northeastern coast of the island (~19°N, 69°W; Berry, 1921). Estimates of the paleoenvironment cannot be made because the fossils sent to Berry from any one locality are too few. All specimens appear to have entire-margined leaves, but they are rendered as line drawings. It would be worthwhile to revisit Sánchez, to see if the fossil-bearing locality still exists, assess the diversity and preservation quality of the megafossils, and determine if the sediments contain plant microfossils. A significant contribution to tropical American vegetation and environmental history would be to survey all the collections made by Berry, Hollick, and others to revise the identifications, record features of leaf physiognomy for leaf margin and CLAMP analysis, and sample the matrix for palynomorphs (Graham, 2003a).[1]

QUATERNARY (~2.6 MA TO PRESENT) = PLEISTOCENE (~2.6 MA–12 KYR) AND HOLOCENE, POST-GLACIAL, OR RECENT (SINCE ~12 KYR)

Megafossils of Pleistocene age are rare in the Antilles, and there are no rodent middens with preserved fruits, seeds, or plant fragments. There are scattered localities from which

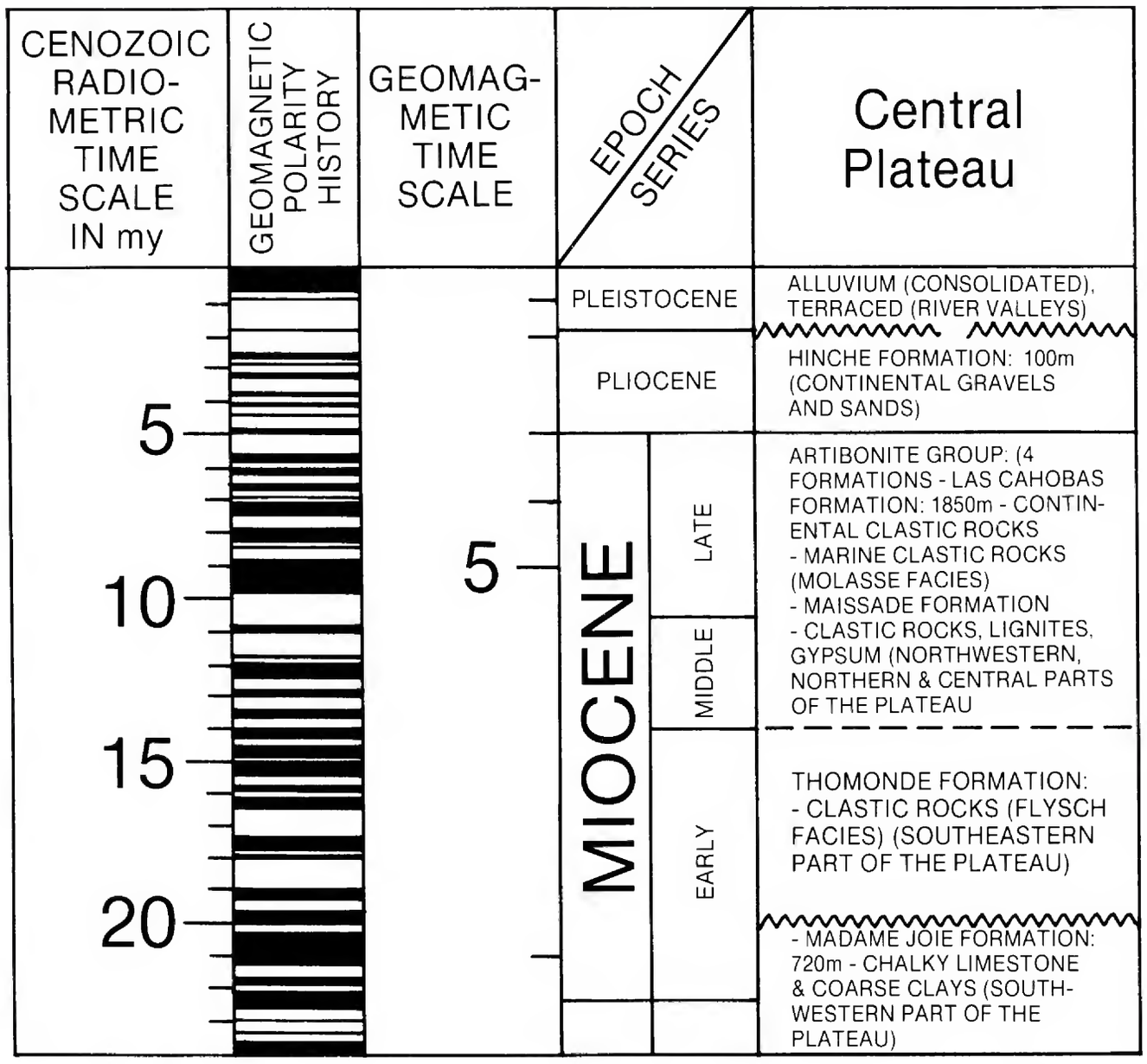


Figure 5.25. Age and stratigraphy of formations in the vicinity of the Miocene Artibonite flora, Haiti. From Bowin (1975). Used with permission of Plenum Publishing Company, New York.

Figure 5.26. Scanning electron microscope photograph of *Pteris* spore from the Miocene Artibonite flora of Haiti.

Figures 5.27, 5.28. Fossil pollen from the Miocene Artibonite flora of Haiti. 5.27. *Hygrophila*. 5.28. *Oryctanthus*.

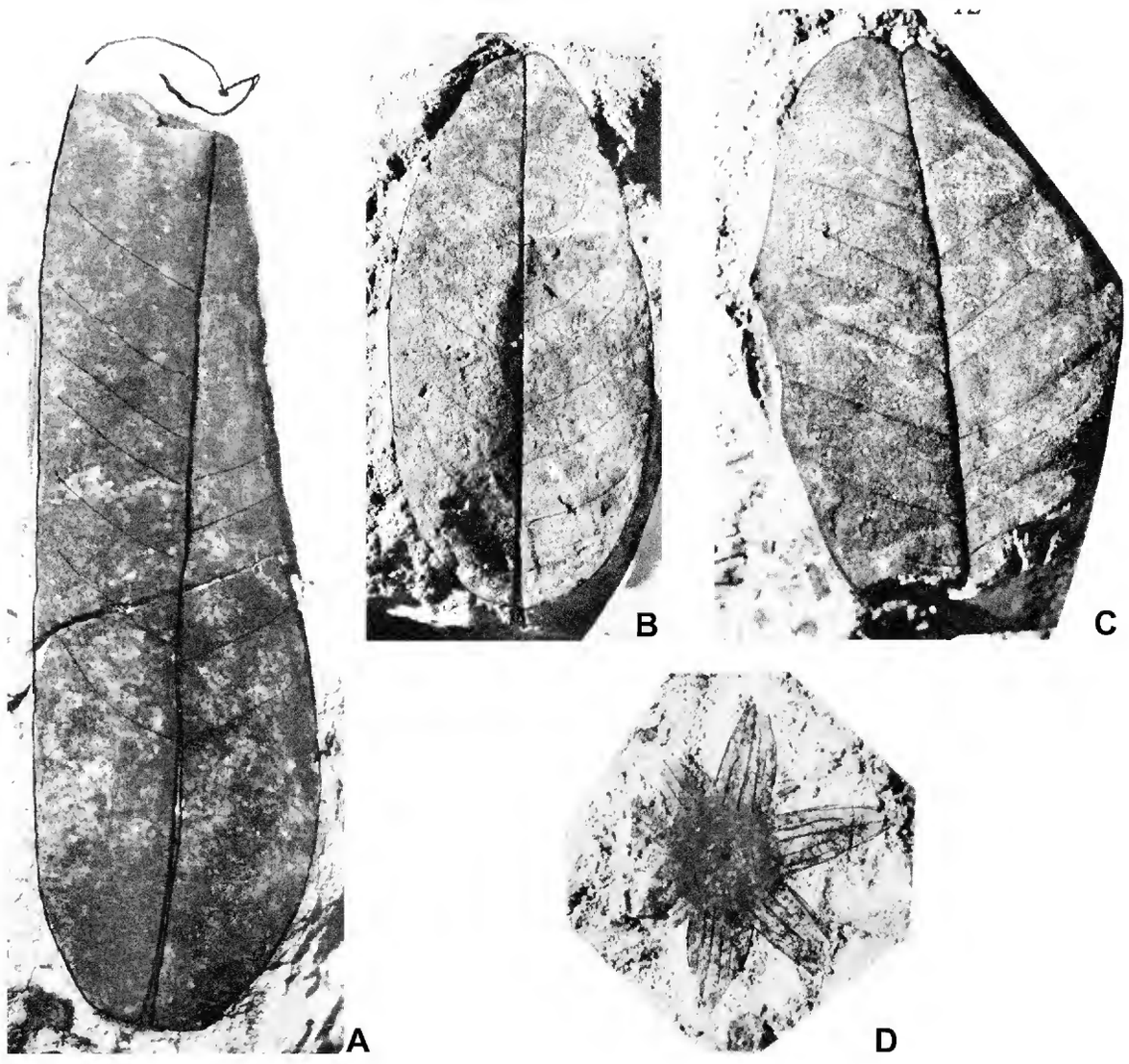


Figure 5.29. Plant megafossils from the Miocene Yumurí flora of Cuba. A. *Pseudolmedia spuria*. B. *Sophora yumuriensis*. C. *Mimusops leonii*. D. *Exostema precaribaeum*. From Berry (1939).

a few plants have been described (Berry, 1934), such as the Chapapote Hot Springs at Baños de Ciego Montero (22°N, 80°W) in Santa Clara Province, Cuba. It contains *Pinus caribaea*, *Juniperus*, *Conocarpus*, and *Mimusops*. Another is an asphalt pit 3 km east of Sabanilla de las Palmas (22°N, 80°W), Matanzas Province, Cuba, where pieces of wood were recovered, along with fruits of *Chrysobalanus icaco* and *Spondias lutea*. All these plants grew in the general region when the fossils were collected in 1911 and 1933. Iturralde-Vinent et al. (2000) have summarized the geology and paleontology of the asphalt seeps in northern Cuba, designated as Las Breas de San Felipe. The age is late Pleistocene or early Holocene, and the plant fossils consist of *Pinus caribaea*, *Calophyllum*, *Chrysobalanus icaco*, *Coccothrinax*, *Cordia galeottiana*, *C. sebestena*, *Ficus*, *Spondias lutea*, and *Thrinax radiata*.

A series of six cores were taken just off the western end of the Isla de la Juventud of Cuba (21°N, 82°W). The sediments are designated as late Pleistocene and are likely late Holocene in age; all palynomorphs represent genera presently growing on the island, with the exception of *Podocarpus*, which grows on adjacent Cuba (fide Moncada Ferrera et al., 1990/91; Table 5.1). The distance between the two islands is presently 96 km across the relatively shallow (~200 m) Gulf of Batabanó, but in glacial times when sea levels were lower by ~120 m, the emergent coastal plains frequently connected or nearly connected the Isla de la Juventud with Cuba. The resolution, age of the sediments, and the data as analyzed do not allow detailed reconstruction of the paleoenvironments, or correlation with sequences in adjacent areas (e.g., the Yucatán and Florida peninsulas). They have not been examined for evidence of Milankovitch cycles, Heinrich events and D–O events, Younger Dryas, Little Ice Age, PGCO, or the Medieval Warm Period (e.g., Fagen, 2000; Chapter 1). There is reason to believe, however, that these events might have affected vegetation in the Antilles and adjacent regions. A ^{14}C-dated core from the Sargasso Sea (27°N, 72°W) showed SSTs ~1° C warmer than at present during the Medieval Warm Period and cooler by ~1° C during the Little Ice Age (Keigwin, 1996). Another study using the relationships between coral (*Montastrea faveolata*) Mg/Ca ratios, coral ^{18}O, seawater ^{18}O, and SST from the southwest coast of Puerto Rico showed SSTs during the Little Ice Age were 2° C cooler and with greater seasonal variation than at present (Watanabe et al., 2001). Lowland vegetation like the present Zapata Swamp likely expanded considerably along the shallow-water southern coast at each glacial maximum when sea levels were lower.

At the Mason River Field Station, Institute of Jamaica, cores were taken from a peat deposit near Kellits in the center of the island. Results have not been published but the cores are at the institute. A core from Lake Miragoâne (18°N, 73°W) on the north side of the southern peninsula of Haiti records the impact of climatic change, fire history, and human settlement on the vegetation (Binford et al., 1987; Brenner & Binford, 1988; Higuera-Gundy, 1989). The lower section of the core reveals cool, dry conditions and a dry mesic forest prior to 10,000 ^{14}C years B.P. There are some similarities with other sequences in northern Latin America, such as the drying trend in the Chihuahuan Desert during this time. Comparisons are limited, however, by the different physical conditions (continental versus insular), and an insufficient number of long cores with the necessary resolution from the Antilles. The dry interval in Haiti was followed by moister climates between 7000 and 3200

^{14}C years B.P., then a drying trend beginning at ~3200 ^{14}C years B.P. The uppermost section of the core dates from 500 years B.P. to the present and shows two periods of forest decline associated with increases in weed pollen and an influx of eroded sediments. One of these periods is between A.D. 1500 and 1700, corresponding to the Spanish occupation of the island, and the other is between 1700 and 1800 at the time of French occupation. Later, there was brief reestablishment of the forest when Haiti became independent in 1804, and large colonial plantations were abandoned in favor of small subsistence farms. The upper 6 cm of the core records events of the past century, including increased human activity (presence of *Zea mays*) and the virtual destruction of the natural vegetation.

Fires and grassland/savanna-like areas in the Antilles—In the Dominican Republic, modern spore and pollen studies from the José del Carmen Ramírez and Armando Bermúdez National Parks provide the basis for paleoecological investigations on the high-altitude vegetation. In the modern pollen rain, the pollen of *Pinus* was present at all localities and ranged from 25%–80%. Other types included fern spores, Cyperaceae, Poaceae, *Garrya*, *Myrica*, and *Myrsine* (Kennedy et al., 2001). The results are important to several aspects of paleovegetation studies, such as assessing the age and naturalness of small local grassy areas (grassland/savanna-like communities) in the highlands. Cores from the La Nevera Sabana of the Juan B. Peréz Rancier National Park (formerly the Valle Nuevo Scientific Reserve; 18°N, 70°W) between 1900 and 2400 m elevation yielded charcoal fragments at 4000 and 9400 ^{14}C years B.P. (Horn et al., 2000). Humans arrived in the Dominican Republic between 6000 and 7000 years B.P. (Rouse & Allaire, 1978; Wilson, 1990, 1997), and sedentary agriculturalists arrived ~2000 years B.P. (Saladoid people; Wilson, 1990). The percentage of *Pinus* pollen was low at intervals containing abundant charcoal fragments (Budzinski et al., 2001). Considering that pine was dominant at all sites in the modern pollen spectra, this suggests the presence of open grassy areas predating the arrival of humans. Thus, the oldest areas are likely natural and resulted mostly from clearings generated by hurricanes and fires ignited by lightning (Chapter 1). It is unknown whether they expanded with the arrival of humans who settled mostly in the lowlands. In Haiti, the highest charcoal concentration corresponds with the dry intervals, indicating that climate was the principal factor. In the lowlands of Puerto Rico, fires were rare prior to human settlement and increased beginning with their arrival at ~4960 ^{14}C years B.P. (Burney et al., 1994). Overall, the pattern of charcoal representation suggests that (1) fires have long been part of the natural ecosystem of the Antilles, (2) they were most prominent during dry climatic intervals, (3) they were important in maintaining scattered open grassy areas, (4) fires increased in the lowlands with the arrival of humans, and (5) they increasingly became a factor later in the highlands with expansion of agriculture and lumbering.

The relationship between fire and human activity has become more complicated in recent times because of greater population pressures and increased land clearing as well as occasional abandonment of the land and return of forests due to changing social or political policies (viz., Puerto Rico, the Haiti record). Also, the present trend to prevent fires that reduce underbrush results in damaging crown fires that periodically expand open vegetation. Although it is likely that grassy areas are part of the long-term natural landscape of the Antilles, their detection from spore and pollen assemblages is difficult because they were mostly ephemeral, scattered, and occupied limited areas where the pollen rain was swamped by surrounding forests. For these reasons, charcoal analysis is important for assessing the history of grassland/savanna-like communities (Horn et al., 2000). In the small island situations of the Antilles, compared to continental settings elsewhere in Latin America, this history does not suggest use of the terms natural grassland or savanna for these grassy openings that have increased in recent times under human influence and likely now occupy their maximum extent.

In the absence of more extensive information on Quaternary vegetation and environmental history from the Antilles, some additional insight may be gained by examining the record from islands just to the north. In the Bahamas (26°–22°N), there are marine terraces 2, 7, and >20 m above sea level (Kindler & Hearty, 2000). The Bahamas Platform is tectonically stable, so the terraces represent times when sea level was higher and, by inference, when climates were warmer. The terraces date from between isotopic stages 13 (528–474 Kyr) and 9 (334–301 Kyr), and probably represent stage 11 (427–364 Kyr), generally regarded as the warmest of the late Quaternary (viz., of the last 500 Kyr). Later in Bermuda during the late interglacial period (substage 5e; Fig. 5.30), conditions were also warmer than at present. The dating and duration of this interval are unsettled, with some investigators suggesting it began ~127 Kyr, while others believe it began 8 Kyr earlier (Muhs et al., 2002). However, it is agreed that a peak in high sea level and warm climate within isotopic substage 5e was reached at ~125 Kyr and that conditions were at least as warm or slightly warmer than at present. This conclusion is supported by the northern range extension of a number of lower latitude marine organisms at this time. MIS 5e was a period of general stability in the Bahamas when coral reefs gradually grew to +2 m above modern sea level. A standstill was reached at +6 and +8.5 m, then sea level fell suddenly to MIS 5d, colder and drier climates prevailed (118 ± 3 Kyr), and extensive dunes developed (Kindler & Strasser, 2000; Hearty & Neumann, 2001). Between 30 and 60 Kyr, SSTs around Bermuda increased abruptly by 2°–5° C, as in the Greenland ice core, followed by cooling (Sachs & Lehman, 1999). If similar changes extended to the islands of the Greater Antilles at 17°–20°N, there must have been frequent expansion and contraction of grassland-like and savanna-like communities.

Glaciation in the Antilles—Structures resembling cirques and moraines in the highest elevations in the Dominican Republic, inferred by Schubert and Medina (1982) from aerial photographs, are cautiously accepted by Orvis et al. (1997, 2002) as evidence for brief episodes of glaciation. In addition

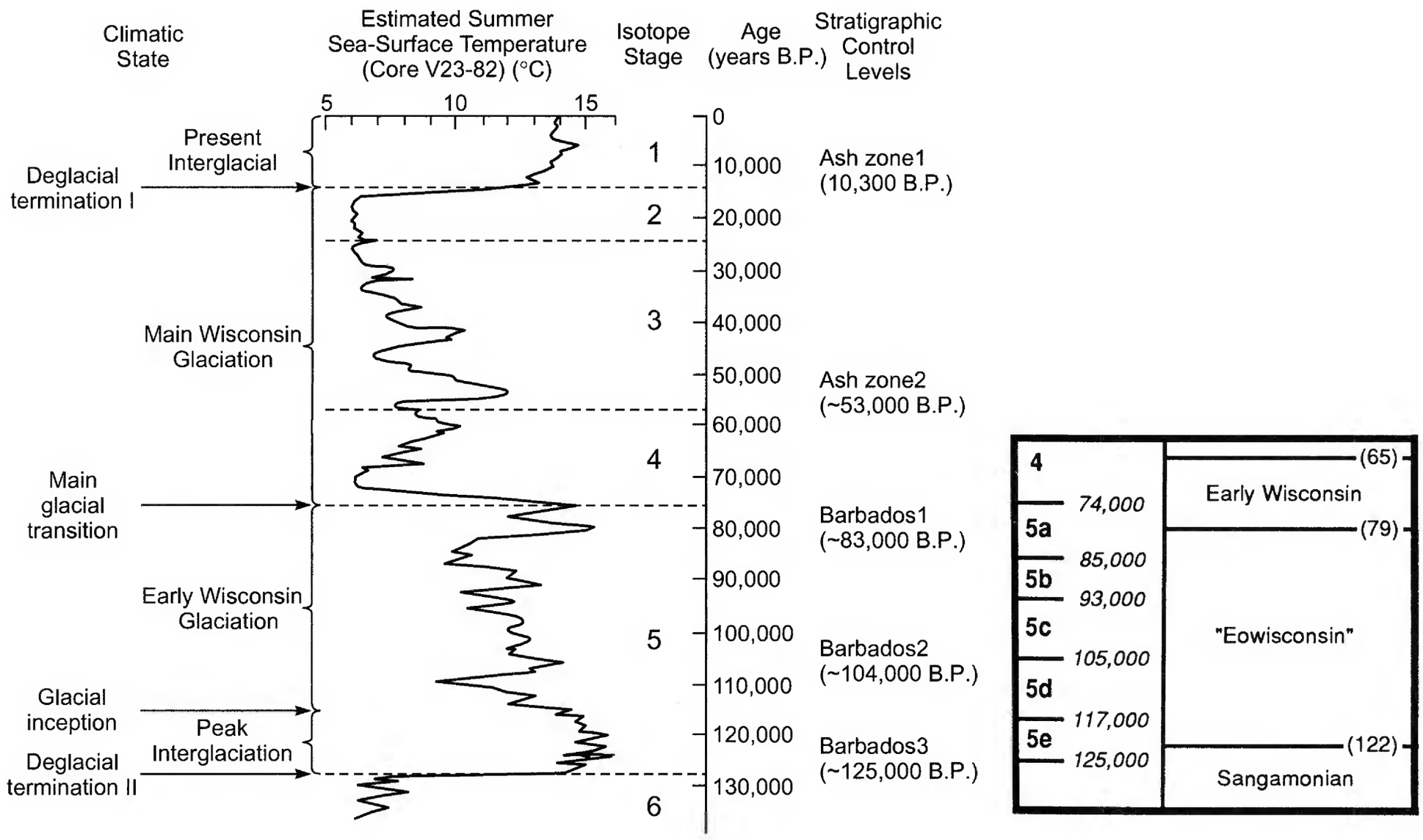


Figure 5.30. Left: Summer sea surface temperatures for the North Atlantic (core V23–82), chronological controls, isotopic stages, and inferred climates. Reprinted from Bradley (1999) and references cited therein, Academic Press, with permission of Elsevier Science Publishers, Amsterdam. Right: Quaternary chronostratigraphic divisions (isotope stages) for the United States and Canada. From Dawson (1992). Reproduced by permission of Taylor & Francis Books, U.K.

to alterations in the physical setting resulting from sea-level fluctuations, such as the width of the coastal plain between adjacent islands and the level of the water tables, the Bermuda high-pressure system was also weakened or displaced during each of the glacial maxima resulting in climates cooler and moister than at present. These changes would be most evident at high elevations and affect vegetation already stressed along ecological gradients, and less evident toward the lowlands where the low latitude, insular environment, and warm equatorial currents mollify changes in climate. Even so, the earlier CLIMAP and COHMAP models that suggested little or no change in MAT in tropical latitudes are now being replaced by ones indicating a lowering of 4°–6° C in the lowlands at glacial maxima. By using a seemingly high lapse rate of 8.5° C/km, Orvis et al. (1997) conclude that glacial conditions would just be reached at ~3000 m altitude.

Summary

The vegetation of the Antilles developed primarily during the past 45 Ma, and its history since that time reflects an insular existence and the climate changes that occurred between the end of the hothouse interval in the Eocene, the transition period of the Oligocene, and the Quaternary glaciations. This history suggests sources of migrants from North America (Hobson, 2002) and from South America with introductions filtered through discontinuous land. This is similar to early conditions in the isthmian region until ~3.5 Ma, when land there became continuous and the continents were connected for the first time since the Cretaceous.

NOTES

1. A potential source of information on Cretaceous, Tertiary, and Quaternary vegetation of the Antilles is lignite and peat. These sediments frequently contain plant microfossils, and their location and age are frequently well known because of their potential economic importance. Robinson (1976, unpublished) identified several of these deposits on Jamaica:

> "Carbonaceous deposits in Jamaica are known to include (a) low grade lignitic sediments and (b) peat. Lignitic beds occur at three stratigraphic levels. The oldest units are Late Cretaceous (70 million years old) and of very limited distribution, associated with Guinea Corn Formation (impure limestones and sandy silts). The most widespread lignitic levels are of early to middle Eocene age (45 million years old) in the Chapelton Formation of Central Jamaica (impure limestones, sands and clays). Other minor occurrences in eastern Jamaica are in the early Eocene Richmond Formation. A single minor lignite

from the Mio–Pliocene August Town Formation (6 million years old) was found.

Relatively small, but significant deposits of peat in Jamaica may offer possibilities of utilization for the generation of electrical power and should be further investigated. Over 14 million tons of peat (assumed 12% moisture basis and 30% ash content) are likely to be present in the Black River Basin and other areas should contain smaller amounts."

REFERENCES

Areces-Mallea, A. E. 1985. Una nueva especie de *Bombacacidites* Couper emend. Krutzsch del Eoceno medio de Cuba. Revista Tecnol. Sér. Geol. 15: 3–7.

———. 1987. Consideraciones sobre la supuesta presencia de *Pinus sylvestris* L. en el Oligoceno de Cuba. Sér. Geol. (Cuba): 2: 27–40.

———. 1988. Palinomorfos de la costa del Golfo de Norteamérica en el Eoceno medio de Cuba. Revista Tecnol. 18: 15–25.

———. 1989. Evidencias de clima Gondwánico en una palinoflora del Cretácico Medio (Cenomaniense) de Cuba occidental. Ci. Tierra Espacio 15–16: 5–66.

———. 1990. *Basopollis krutz[s]chi* Kedves: Primera determinación de un normapolles en el Paleógeno de Cuba. Ci. Tierra Espacio 17: 27–40.

Berner, R. A. and G. P. Landis. 1988. Gas bubbles in fossil amber as possible indicators of the major gas composition of ancient air. Science 239: 1406–1409.

Berry, E. W. 1921. Tertiary fossil plants from the Dominican Republic. Proc. U. S. Natl. Mus. 59: 117–127.

———. 1923. Tertiary fossil plants from the Republic of Haiti. Proc. U. S. Natl. Mus. 62: 1–10.

———. 1934. Pleistocene plants from Cuba. Bull. Torrey Bot. Club 61: 237–241.

———. 1939. A Miocene flora from the Gorge of the Yumurí River, Matanzas, Cuba. Johns Hopkins Univ. Stud. Geol. 13: 95–136.

Binford, M. W. et al. (+ 5 authors). 1987. Ecosystems, paleoecology and human disturbance in subtropical and tropical America. Quatern. Sci. Rev. 6: 115–128.

Bowin, C. 1975. The geology of Hispaniola. *In:* E. M. Narin and F. G. Stehli (eds.), The Ocean Basins and Margins. Plenum, New York. pp. 501–552.

Bradley, R. S. 1999. Paleoclimatology: Reconstructing Climates of the Quaternary. 2nd ed. Harcourt, Academic Press, New York.

Brenner, M. and M. W. Binford. 1988. A sedimentary record of human disturbance from Lake Miragoane, Haiti. J. Paleolimnol. 1: 85–97.

Brodie, C. 2005. Rock of ages, could a single cell live for 250 million years? Amer. Sci. 93: 503–504.

Budzinski, K. M., S. P. Horn, L. M. Kennedy, and K. H. Orvis. 2001. A 5000-year pollen and macroscopic charcoal record from the highlands of the Dominican Republic. Abstract, Annual Meeting of the Association of American Geographers, New York (2001). p. 1.

Burney, D. A., L. P. Burney, and R. D. E. MacPhee. 1994. Holocene charcoal stratigraphy from Laguna Tortuguero, Puerto Rico, and the timing of human arrival on the island. J. Archaeol. Sci. 21: 273–281.

Cano, R. J. and M. K. Borucki. 1995. Revival and identification of bacterial spores in 25- to 40-million-year-old Dominican amber. Science 268: 1060–1064.

Cousminer, H. L. 1957. Paleontological report, sample 65-A, Collazo No. 1 well. Archivos del Fondo Geológico Nacional de Cuba. Unpublished.

Dawson, A. G. 1992. Ice Age Earth: Late Quaternary Geology and Climate. Routledge, London.

Dilcher, D. L., P. S. Herendeen, and F. Hueber. 1992. Fossil *Acacia* flowers with attached anther glands from Dominican Republic amber. *In:* P. S. Herendeen and D. L. Dilcher (eds.), Advances in Legume Systematics 4: The Fossil Record. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 33–42.

Fagen, B. M. 2000. The Little Ice Age: How Climate Made History, 1300–1850. Basic Books, New York.

Gómez, L. D. 1982. *Grammitis succinea*, the first New World fern found in amber. Amer. Fern J. 72: 49–52.

Graham, A. 1990. Late Tertiary microfossil flora from the Republic of Haiti. Amer. J. Bot. 77: 911–926.

———. 1993. Contribution toward a Tertiary palynostratigraphy for Jamaica: The status of Tertiary paleobotanical studies in northern Latin America and preliminary analysis of the Guys Hill Member (Chapelton Formation, middle Eocene) of Jamaica. *In:* R. M. Wright and E. Robinson (eds.), Biostratigraphy of Jamaica. Geol. Soc. Amer. Mem.: 443–461.

———. 1996. Paleobotany of Puerto Rico, from Arthur Hollick's (1928) Scientific Survey paper to the present. Ann. New York Acad. Sci. 776: 103–114.

———. 1999. The Tertiary history of the northern temperate element in the northern Latin American biota. Amer. J. Bot. 86: 32–38.

———. 2003a. The concepts of deep-time floras and paleobotanical hotspots. Syst. Bot. 28: 461–464.

———. 2003b. Historical phytogeography of the Greater Antilles. Brittonia 55: 372–398.

———, D. Cozadd, A. Areces-Mallea, and N. O. Frederiksen. 2000. Studies in Neotropical paleobotany. XIV. A palynoflora from the middle Eocene Saramaguacán Formation of Cuba. Amer. J. Bot. 87: 1526–1539.

——— and D. M. Jarzen. 1969. Studies in Neotropical paleobotany. I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308–357.

Habib, D. 1969. Middle Cretaceous palynomorphs in a deep-sea core from the seismic reflector Horizon A outcrop area. Micropaleontology 15: 85–101.

Hearty, P. J. and A. C. Neumann. 2001. Rapid sea level and cli-

mate change at the close of the Last Interglaciation (MIS 5e): Evidence from the Bahama Islands. Quartern. Sci. Rev. 20: 1881–1895.

Hedges, S. B. 2001. Biogeography of the West Indies: An overview. *In:* C. A. Woods and F. E. Sergile (eds.), Biogeography of the West Indies: Patterns and Perspectives. 2nd ed. CRC Press, Boca Raton. pp. 15–33.

———. 2006. Historical zoogeography of the West Indies. *In:* A. Graham (ed.), The Biogeography of Latin America—Causes and Effects. Ann. Missouri Bot. Gard. 93: 231–244.

Higuera-Gundy, A. 1989. Recent vegetation changes in southern Haiti. *In:* C. A. Woods (ed.), Biogeography of the West Indies. Sand Hill Crane Press, Gainesville, FL. pp. 191–200.

Hobson, K. A. 2002. Incredible journeys. Science 295: 981–983.

Hollick, A. 1928. Paleobotany of Porto Rico. New York Academy of Sciences Scientific Survey of Porto Rico and the Virgin Islands 7: 177–393.

Horn, S. P., K. H. Orvis, L. M. Kennedy, and G. M. Clark. 2000. Prehistoric fires in the highlands of the Dominican Republic: Evidence from charcoal in soils and sediments. Caribbean J. Sci. 36: 10–18.

Hueber, F. M. and J. Langenheim. 1986. Dominican amber tree had African ancestors. Geotimes 31: 8–10.

Iturralde-Vinent, M. A. 2001. Geology of the amber-bearing deposits of the Greater Antilles. Caribbean J. Sci. 37: 141–167.

——— and E. Hartstein. 1998. Miocene amber and lignitic deposits in Puerto Rico. Caribbean J. Sci. 34: 308–312.

——— and R. D. E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science 273: 1850–1852.

——— and ———. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. Bull. Amer. Mus. Nat. Hist. 238: 1–95.

——— et al. (+ 5 authors). 2000. Las Breas de San Felipe, a Quaternary fossiliferous asphalt seep near Martí (Matanzas Province, Cuba). Caribbean J. Sci. 36: 300–313.

Keigwin, L. D. 1996. The Little Ice Age and Medieval Warm Period in the Sargasso Sea. Science 274: 1504–1508.

Kennedy, L. M., S. P. Horn, and K. H. Orvis. 2001. Modern pollen spectra from the highlands of the Cordillera Central, Dominican Republic. Rev. Palaeobot. Palynol. 137: 51–68.

Kesler, S. E., N. Russell, J. Polanco, K. McCurdy, and G. L. Cumming. 1991. Geology and geochemistry of the Early Cretaceous Los Ranchos Formation, central Dominican Republic. *In:* P. Mann, G. Draper, and J. F. Lewis (eds.), Geologic and Tectonic Development of the North American–Caribbean Plate Boundary in Hispaniola. Geol. Soc. Amer. Spec. Paper 262: 187–202.

Kindler, P. and P. J. Hearty. 2000. Elevated marine terraces from Eleuthera (Bahamas) and Bermuda: Sedimentological, petrographic and geochronological evidence for important deglaciation events during the middle Pleistocene. Global Planet. Change 24: 41–58.

——— and A. Strasser. 2000. Palaeoclimatic significance of co-occurring wind- and water-induced sedimentary structures in the last-interglacial coastal deposits from Bermuda and the Bahamas. Sedimentary Geol. 131: 1–7.

MacLeod, K. G., B. T. Huber, and M. L. Ducharme. 2000. Paleontological and geochemical constraints on the deep ocean during the Cretaceous greenhouse interval. *In:* B. T. Huber, K. G. MacLeod, and S. L. Wing (eds.), Warm Climates in Earth History. Cambridge University Press, Cambridge, U.K. pp. 241–274.

Maurrasse, F. J-M. R. 1982. Survey of the Geology of Haiti, Guide to the Field Excursions in Haiti, March 3–8, 1982. Miami Geological Society, Miami.

Moncada Ferrera, M., C. E. Hernández Fuentes, and M. Cabrera Castellanos. 1990/1991. Análisis polínico de sedimentos marinos del occidente de la Isla de La Juventud (Cuba). Acta Bot. Hung. 36: 145–161.

Muhs, D. R., K. R. Simmons, and B. Steinke. 2002. Timing and warmth of the last interglacial period: New U-series evidence from Hawaii and Bermuda and a new fossil compilation for North America. Quartern. Sci. Rev. 21: 1355–1383.

Orvis, K. H., G. M. Clark, S. P. Horn, and L. M. Kennedy. 1997. Geomorphic traces of Quaternary climates in the Cordillera Central, Dominican Republic. Mountain Res. Developm. 17: 323–331.

———, S. P. Horn, and G. M. Clark. 2002. The case for Late-Pleistocene glaciers on Hispaniola. Abstract, Annual Meeting of the Association of American Geographers, Los Angeles (2002). p. 1.

Poinar, G. O., Jr. 2002. Fossil palm flowers in Dominican and Mexican amber. Bot. J. Linn. Soc. 138: 57–61.

——— and R. Singer. 1990. Upper Eocene gilled mushroom from the Dominican Republic. Science 248: 1099–1101.

——— and G. M. Thomas. 1982. An entomophthoralean fungus from Dominican amber. Mycologia 74: 332–334.

Raven, P. H. and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

Robinson, E. 1976. Lignite in Jamaica, with additional remarks on peat. A Report to the Capital Development Fund, from the Ministry of Mining and Natural Resources, Kingston. 27 pp. Unpublished.

——— and S. F. Mitchell. 1999. Upper Cretaceous to Oligocene stratigraphy in Jamaica. *In:* S. F. Mitchell (ed.), Contributions to Geology, No. 4. Department of Geography and Geology, University of the West Indies, Mona, Kingston. pp. 1–47.

Rouse, I. and L. Allaire. 1978. Caribbean. *In:* R. E. Taylor and C. W. Meighan (eds.), Chronologies in New World Archaeology. Academic Press, New York. pp. 431–481.

Sachs, J. P. and S. J. Lehman. 1999. Subtropical North Atlantic temperatures 60,000 to 30,000 years ago. Science 286: 756–759.

Sánchez-Baracaldo, P. 2004. Phylogenetics and biogeography of the Neotropical fern genera *Jamesonia* and *Eriosorus* (Pteridaceae). Amer. J. Bot. 91: 274–284.

Schubert, C. and E. Medina. 1982. Evidence of Quaternary glaciation in the Dominican Republic: Some implications for Caribbean paleoclimatology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 39: 281–294.

Smiley, C. J. 1982. Cretaceous plants from the Dominican Republic. Unpublished report to Rosario Dominicana. 20 pp.

———. 2002. Lower Cretaceous plants from the Dominican Republic. *In:* T. A. Jackson (ed.), Caribbean Geology into the Third Millennium. Transactions of the 15th Caribbean Geological Conference, University of the West Indies, Mona, Kingston. pp. 119–129.

Stubblefield, S. P., C. E. Miller, T. N. Taylor, and G. T. Cole. 1985. *Geotrichites glaesarius*, a conidial fungus from Tertiary Dominican amber. Mycologia 77: 11–16.

Watanabe, T., A. Winter, and T. Oba. 2001. Seasonal changes in sea surface temperature and salinity during the Little Ice Age in the Caribbean Sea deduced from Mg/Ca and $^{18}O/^{16}O$ ratios in corals. Mar. Geol. 173: 21–35.

Wilson, S. M. 1990. Hispaniola: Caribbean Chiefdoms in the Age of Columbus. University of Alabama Press, Tuscaloosa.

——— (ed.). 1997. The Indigenous People of the Caribbean. University of Florida Press, Gainesville.

ADDITIONAL REFERENCES/GENERAL READINGS

Amber/Ancient DNA

Fishman, J. 1995. Have 25-million-year-old bacteria returned to life? Science 268: 977.

Grimaldi, D. 1992. Review: G. O. Poinar Jr. 1992. Life in Amber. Stanford University Press, Stanford, CA. Science 258: 1822.

———. 1996. Amber: Window to the Past. Harry N. Abrams Publishers, in association with the American Museum of Natural History, New York.

———. 2000. Review: G. Poinar Jr. and R. Poinar. 1999. The Amber Forest: A Reconstruction of a Vanished World. Princeton University Press, Princeton, NJ. Quart. Rev. Biol. 75: 445–446.

Hedges, S. B. 1999. Review: G. Poinar Jr. and R. Poinar. 1999. The Amber Forest: A Reconstruction of a Vanished World. Princeton University Press, Princeton, NJ. Nature 402: 459.

Holden, C. 1997. "No go" for Jurassic Park-style dinos. Science 276: 361.

Langenheim, J. H. 1969. Amber: A botanical inquiry. Science 163: 1157–1169.

MacPhee, R. D. E. and D. A. Grimaldi. 1996. Mammal bones in Dominican amber. Nature 380: 489–490.

Penney, D. 2005. Importance of Dominican Republic amber for determining taxonomic bias of fossil resin preservation—A case study of spiders. Palaeogeogr. Palaeoclimatol. Palaeoecol. 223: 1–8.

Poinar, G. O., Jr. 1992. Life in Amber. Stanford University Press, Stanford, CA.

——— and R. Poinar. 1999. The Amber Forest: A Reconstruction of a Vanished World. Princeton University Press, Princeton, NJ. [See reviews by Grimaldi, 2000; Hedges, 1999.]

Rice, P. C. 1993. Amber: The Golden Gem of the Ages. The Kosciuszko Foundation, New York.

Ross, J. F. 1993. Treasured in its own right, amber is a golden window on the long ago. Smithsonian 23: 31–41.

Santiago-Blay, J. A. and J. B. Lambert. 2007. Amber's botanical origins revealed. Amer. Sci. 95: 148–157.

Sykes, B. 1997. Lights turning red on amber. Nature 386: 764–765.

Wilson, E. O. 1985. Invasion and extinction in the West Indian ant fauna: Evidence from the Dominican Amber. Science 229: 265–267.

Other References/Readings

Bralower, T. J. et al. (+ 7 authors). 1997. High-resolution records of the late Paleocene thermal maximum and circum-Caribbean volcanism: Is there a causal link? Geology 25: 963–966.

Coleman, M., A. Liston, J. W. Kadereit, and R. J. Abbott. 2003. Repeated intercontinental dispersal and Pleistocene speciation in disjunct Mediterranean and desert *Senecio* (Asteraceae). Amer. J. Bot. 90: 1446–1454.

Hollick, A. 1924. A revision of the fossil flora of the West Indies, with descriptions of new species. New York Bot. Gard. Bull. 12: 259–323.

Iturralde-Vinent, M. A. (ed.). 2004. Origen y Evolución del Caribe y sus Biotas Marinas y Terrestres. CD-ROM, Centro Nacional Información Geológica, Habana, Cuba. [Tectónica de placas, Paleogeografía, Plants fósiles, Ambar Antillano, Biogeografía.]

Kennedy, L. M., S. P. Horn, and K. H. Orvis. 2006. A 4000-year record of fire and forest history from Valle de Bao, Cordillera Central, Dominican Republic. Palaeogeogr. Palaeoclimatol. Palaeoecol. 231: 279–290.

MacPhee, R. D. E. 2005. "First" appearances in the Cenozoic land-mammal record of the Greater Antilles: Significance and comparison with South American and Antarctic records. J. Biogeogr. 32: 551–564.

Pajón, J. M., I. Hernández, F. Ortega, and J. Macle. 2001. Period of wet climate in Cuba: Evaluation of expression in karst of Sierra de San Carlos. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 217–226.

Roca, A. L. (+ 7 authors). 2004. Mesozoic origin for West Indian insectivores. Nature 429: 649–651.

Watters, D. R. and R. B. Miller. 2000. Wood identification in historic sites: Inferences for colonial trade and modification of vegetation on Barbuda. Caribbean J. Sci. 36: 19–30.

Chapter 6

CENTRAL AMERICA

GUATEMALA/NICARAGUA/BELIZE/ EL SALVADOR

CRETACEOUS (?)

Megafossils—Two Late Cretaceous plants, *Araucarites* sp. and *Dicksoniopsis conipteroides*, were described by Stephenson and Berry (1929) from Chipaxché, Verapaz, Guatemala (Figs. 6.1, 6.2; Table 6.1). The assemblage hardly qualifies as a flora, but it is noteworthy as the only Cretaceous plant material published for Central America. There has been no further field reconnaissance for additional specimens, it is not known if microfossils are present, and neither the age of the flora nor the identifications have been confirmed.

MIO–PLIOCENE

Microfossils—The only pre-Quaternary paleobotanical floras published for Guatemala are Neogene microfossils from the Padre Miguel Group and the Herrería Formation (Graham, 1998, 2006). The two localities in the Padre Miguel Group (15°45'N, 88°42'W; F and G in Fig. 6.3; Fig. 6.4) are on the Maya Block north of the Motagua–Polochic Fault Zone that separates the North and South American plates. The two localities in the Herrería Formation (14°43'N, 89°29'W; designated B and 4 on Fig. 6.3) are on the Chortis Block south of the boundary. The stratigraphic relationships between the formations are not well established, but the Padre Miguel Group is older (probably late Miocene to Mio–Pliocene), and the Herrería Formation is probably Pliocene in age (Fig. 6.5).

The composition and numerical representations of the two floras are given in Table 6.2, and representative microfossils are illustrated in Figs. 6.6–6.15. The Padre Miguel is an upland assemblage that includes pollen of *Picea* (no longer present in Guatemala, Fig. 6.8), *Pinus* (Fig. 6.7), *Alfaroa–Oreomunnea* (Fig. 6.11), *Juglans* (Fig. 6.12), *Quercus* (Figs. 6.13, 6.14), and *Ulmus* (Fig. 6.15). With the exception of the warm-temperate *Alfaroa–Oreomunnea*, these are all northern temperate elements also found in the middle Eocene Claiborne Group of the southeastern United States and in the middle Pliocene Paraje Solo Formation of southeastern Mexico. However, at the latter site they occur in greater abundance and diversity (e.g., with *Abies*, *Alnus*, *Liquidambar*, *Myrica*, *Populus*, and *Smilax*). This apparent trend in the later arrival of northern temperate elements southward in diminishing numbers will be assessed further after other paleofloras are described from Central America and northern South America.

The Herrería assemblage is a coastal lowland flora as shown by the dinoflagellate *Operculodinium* (*Gonyaulax grindleyi* [*Protoceratium reticulatum*]), *Rhizophora* pollen reaching nearly 100% in one sample, and abundant spores of cf. *Acrostichum* (Fig. 6.6, maximum percentage among the samples 45%, probably representing the mangrove fern *A. aureum*).

Estimates of the paleoenvironment from such a limited paleobotanical database must incorporate evidence from a variety of sources and be evaluated within the context of regional trends in sea levels and temperature. The inland Mio–Pliocene Padre Miguel flora with a prominent representation of northern temperate elements, including *Picea*, grew under temperatures estimated ~2°–3° C cooler than at present. In contrast, the representation of marine and brackish-water elements in the Herrería assemblage was likely due to warmer MATs making for higher sea levels that inundated the site. Tectonic activity may have raised or lowered the land during the same interval. If the inundation was due at least in part to a eustatic rise in sea level, then the middle Pliocene would be a propitious time because global temperatures were ~3.5° C higher than at present, and there was a rise in sea level of 35 ± 18 m along the southeastern U.S. Atlantic Coastal Plain (Fig. 6.16; Dowsett & Cronin, 1990). The current MAT at Puerto Barrios (essentially at sea level) is 26.9° C and in the middle Pliocene it may have been slightly warmer. These trends and estimates are consistent with other lines of evidence, but additional paleobotanical information is necessary to reconstruct the vegetation and environments more precisely.

The plant formations represented in the Padre Miguel Group and the Herrería Formation are mangrove (cf. *Acrostichum*, *Rhizophora*), herbaceous bog/marsh/swamp (a sedge marsh; Cyperaceae, 29%, possibly with palms and ferns), lower to upper montane broad-leaved forest (*Alfaroa–Oreomunnea*) with a northern temperate element association (*Juglans*, *Ulmus*), coniferous and pine-oak forest (*Pinus*, *Quercus*), and high-altitude coniferous forest (*Pinus*, *Picea*). There is no evidence for desert, shrubland/chaparral–woodland–savanna (*Iresine* and some species of *Caesalpinia* are found in open, drier habitats; Asteraceae in several plant formations), grassland (maximum grass pollen 8%), lowland Neotropical rain forest, or páramo. This is consistent with the geology indicating moderate elevations, and with other fossil floras of the region. There were probably beach/strand/dune and aquatic communities present, but they were not recorded in the microfossil floras.

In Nicaragua, it is remarkable that the plant fossil record for the Late Cretaceous through the Quaternary consists of one

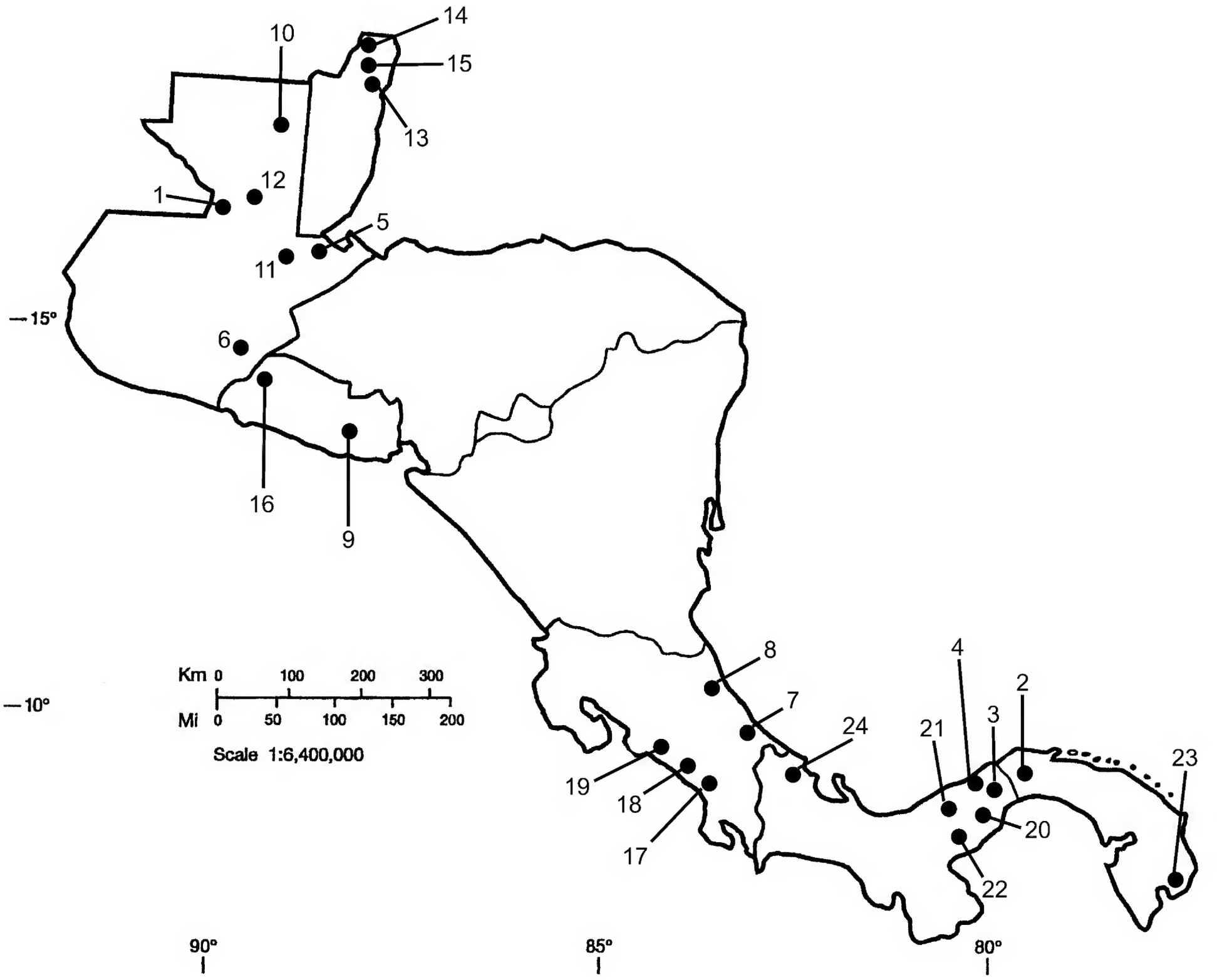


Figure 6.1. Location of fossil floras of Central America mentioned in the text. Cretaceous (?): 1 = Chipaxché; Eocene: 2 = Gatuncillo; Miocene: 3 = Culebra, Cucaracha, La Boca, 4 = Gatún; late Miocene to Mio–Pliocene: 5 = Padre Miguel; Pliocene: 6 = Herrería, 7 = Sheroli, 8 = Zent; Plio–Pleistocene: 9 = Sisimico–Tal; Quaternary: 4 = Gatún Lake, 10 = Lake Salpeten, Lake Petén–Itzá, Laguna Petenxil, Lake Quexil, 11 = Lake Izabal, 12 = Laguna Tamarindito, 13 = Cobweb Swamp, 14 = Laguna Cocos, 15 = Pulltrouser Swamp, 16 = Lake Guija, Lake Cuscachapa, 17 = Río General, 18 = Lachner Bog, 19 = La Chonta, 20 = El Valle, 21 = La Yeguada, 22 = Cueva de los Ladrones, 23 = Darién (Cana), 24 = Changuinola.

megafossil (*Prioria tufficola*) described from modern deposits near San Rafael (Brown, 1947; Graham, 2001). Two depositional processes favorable to the preservation of fossil floras were occurring in eastern Nicaragua during the Tertiary. A receding coastline along the relatively passive Atlantic–Caribbean margin undoubtedly allowed accumulation of spore and pollen-bearing lignites and fine-grained sediments like those of eastern Mexico and Guatemala. Also, volcanic activity in the mountains of northern and western Nicaragua provided ash to form fine-grained shales and tuffs that likely contain plant megafossils. Indeed, one such locality is known from the general region of Las Mesetas de los Pueblos where the mesetas are composed of ash that is cut into blocks (canteras) and used for construction. Sediments from a well dug through the ash contained plant megafossils, but they have not been studied (Warren Stevens & Olga Martha Montiel, pers. comm., 2003). Cores from Lake Nicaragua would be valuable, but difficult to obtain, and the interpretations complicated by the size of the lake, the largest in Central America, and because it is essentially a closed bay near the Pacific coast that must have been inundated frequently in the past. However, with improving drilling and interpretative methods, it is likely that such a project will be initiated in the future.

A flora of Plio–Pleistocene age is described by Lötschert and Mädler (1975) from the Cuscatlán Sequence of El Salvador (Table 6.1). The megafossils are lowland tropical in composition, while the microfossils include representatives from the uplands such as *Pinus*, cf. *Abies*, *Carya*, *Celtis*, *Juglans*, *Quercus*, *Ulmus* type, and, unexpectedly, the presently Asiatic *Pterocarya*[?], which disappeared from northern North America

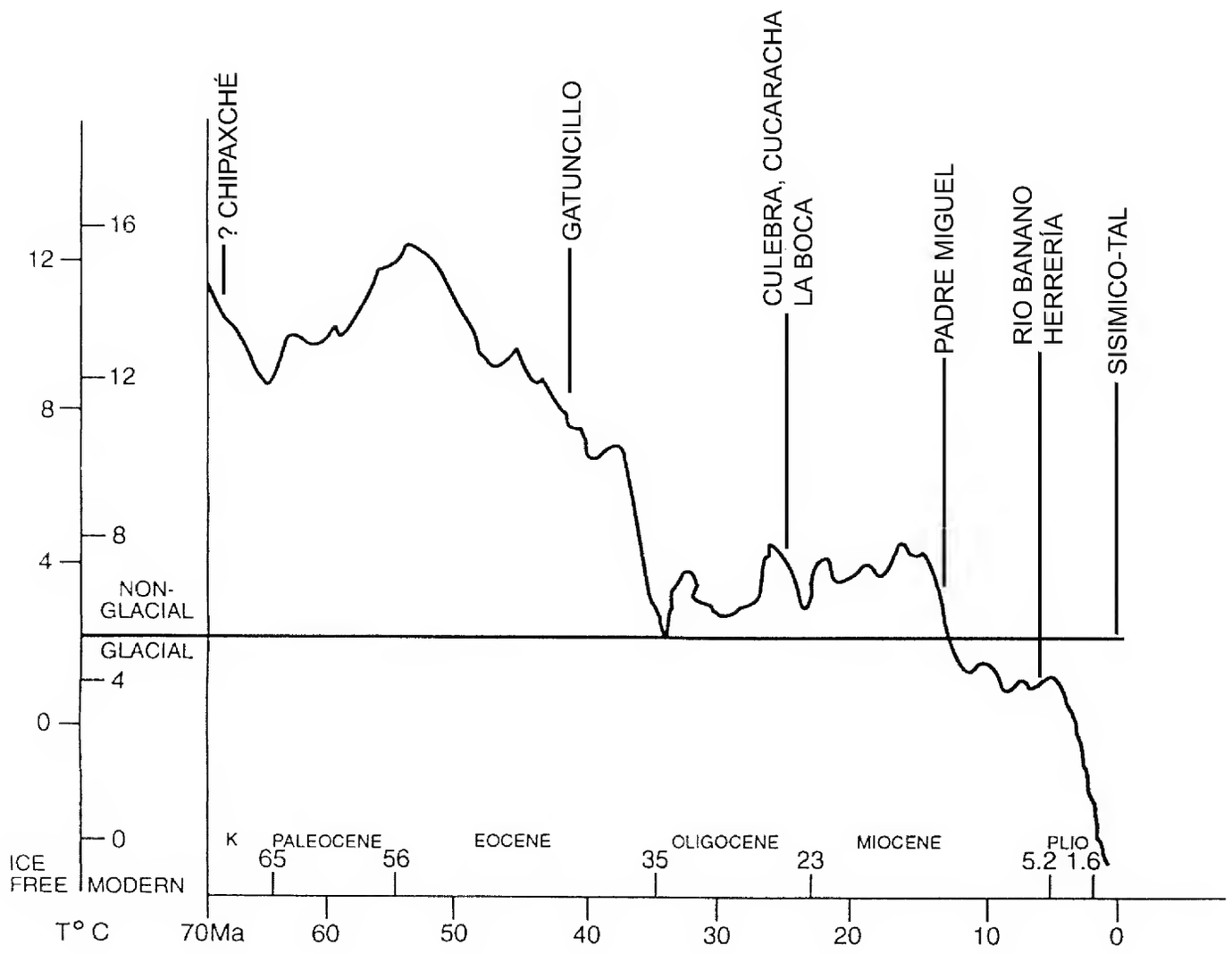


Figure 6.2. Global paleotemperature curve with Tertiary floras of Central America.

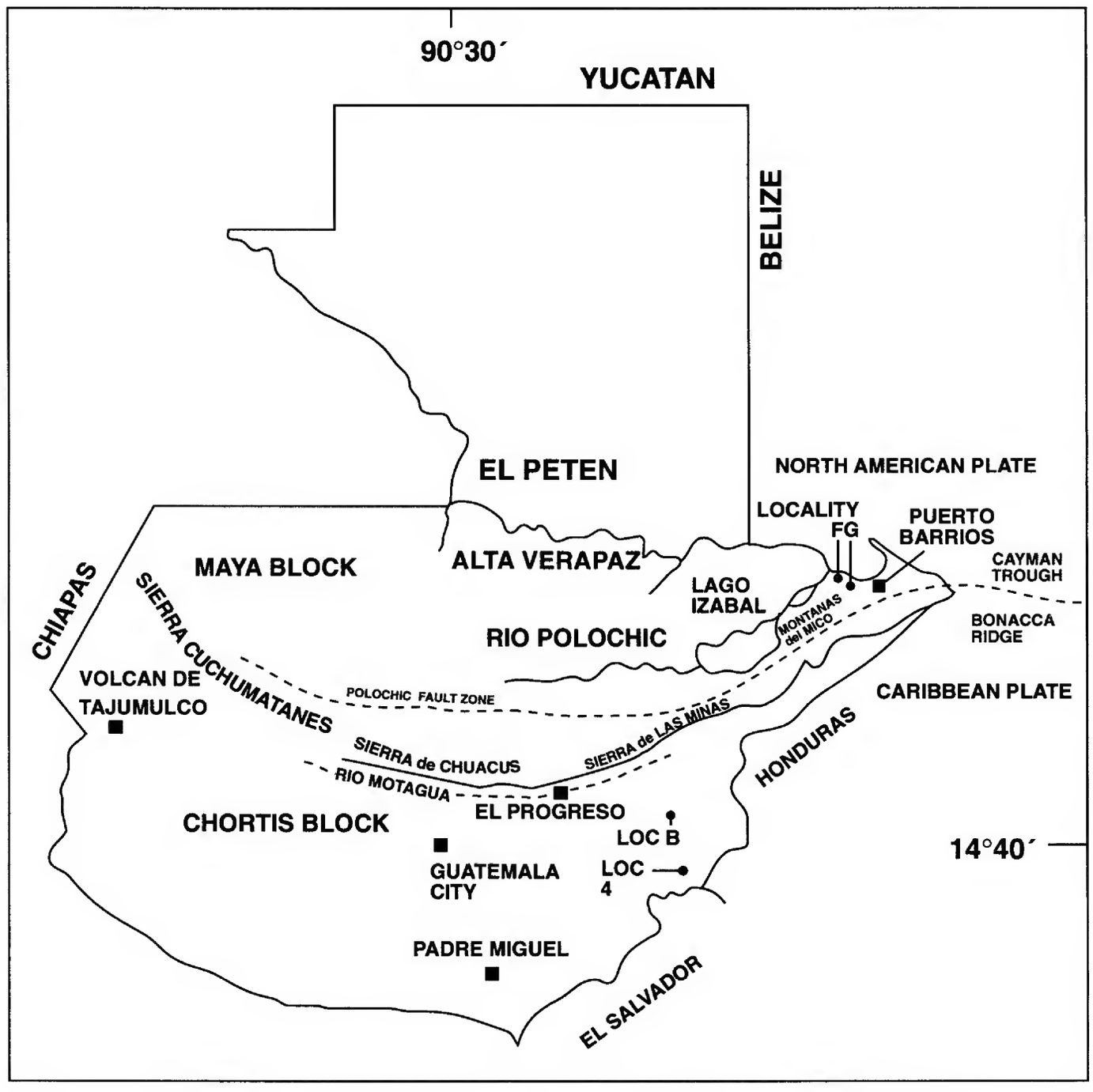


Figure 6.3. Index map of place names and localities for paleobotanical sites in Guatemala.

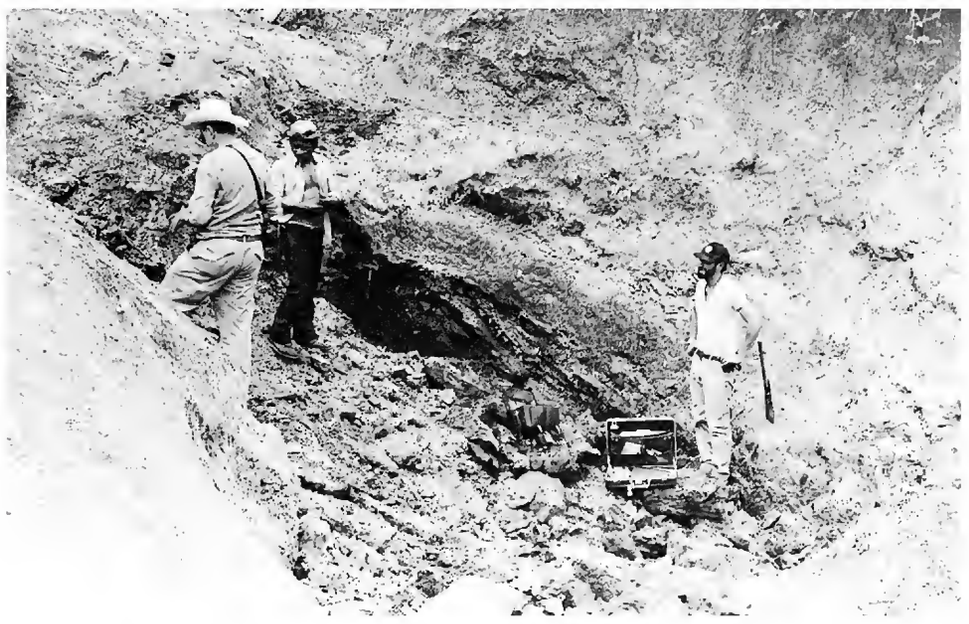


Figure 6.4. Collecting locality F in the Herrería Formation of Guatemala. The dark lens in the center of the picture is a layer of lignite from which most of the plant microfossils came. Above and below the lignite are layers of fine-grained mineral sediments (clay, siltstones, with plant microfossils) and fine-grained sandstones marking slight shifts in water depth/distance from shoreline resulting from inundation and regression.

in the Pliocene. Otherwise the flora is similar to the extant vegetation of northern Central America.

QUATERNARY

Much of the early work on past vegetation and environments in Guatemala focused on the Quaternary record in the Maya lowlands of the Petén (Hutchinson & Goulden, 1966; Tsukada & Deevey, 1967 [including lakes Guija and Cuscachapa in El Salvador]; Deevey, 1978; Vaughan et al., 1985). Projects continue there, and in the Yucatán Peninsula of Mexico (see Leyden, 2002; Islebe & Leyden, 2006), making the Quaternary of the region one of the most intensively studied paleobotanical hotspots in Latin America. An important contribution has been to define the spore and pollen signatures for both the Guatemalan uplands (Islebe & Hooghiemstra, 1995; Fig. 6.17) and the lowlands (Leyden, 2002; Fig. 6.18). Collectively, they give the spectra for alpine, subalpine, fir, evergreen, deciduous, and dry forests, and for savannas. The Guatemalan profile shows, for example (Fig. 6.18), that the ecology of *Curatella* (*C. americana*, Chapter 3) and the dispersal characteristics of its pollen closely associate the modern genus with savanna, and that its fossil pollen is a strong indicator of that ecosystem. The same is true for *Byrsonima* (*B. crassifolia*). In contrast, the pollen signature data show that although *Brosimum alicastrum* in Guatemala is primarily an evergreen tree of moist forests, it and its pollen are also found in drier communities. Therefore, an accurate assessment of its paleoecological significance in pollen diagrams requires corroborative evidence. There are no spore and pollen diagrams from the highlands of Guatemala, but the Cordillera de Cuchumatanes was glaciated at the LGM with an ELA of 3655–3544 m, or 1300–1500 m lower than at present (Lachniet & Vázquez-Selem, 2005).

An early contribution of particular interest in reconstructing the late Quaternary paleoenvironmental and vegetation history for the lowlands of Guatemala was by Leyden (1984, 2002; Lake Salpeten, Figs. 6.19, 6.20). It revealed an interval of late Pleistocene aridity (savanna and juniper shrub, halophytic marshes; ~11,000 years B.P.), an interval that is now widely recognized in the Petén (e.g., Lake Quexil; Leyden et al., 1993) and elsewhere in Latin America. This is relevant to later discussions about whether the lowland Neotropical rain forest experienced coolness, or both coolness and dryness during the Quaternary. Evidence is building that it was the latter, along with changes in sea level that must also have affected low-lying areas.

In the Laguna Verde (13°53'N, 89°53'W), located in the crater of a stratovolcano in the Sierra de Apaneca of El Salvador, the sediments preserve a record of vegetation and climate change for the past 8000 years B.P. (Dull, 2004). Between 8000 and 5000 years B.P., during the mid-Holocene warm period, lowland tropical plants extended an estimated 200–250 m higher than at present, suggesting a MAT warmer by ~1.0° C. Pollen of cloud forest genera such as *Alnus*, *Juglans*, *Liquidambar*, and *Ulmus* was also abundant. At ~5500 years B.P., Holocene cooling with drying resumed until ~3500 years B.P., when modern forests were established. Within this period, pollen of weeds is found at ~5000 years B.P., and *Zea* at 4440 years B.P. A reduction in agricultural-disturbance vegetation occurred at ~1520 years B.P. corresponding to the eruption of Volcán Ilopango.

In summarizing the data for the Maya lowlands of Guatemala and Belize (Cobweb Swamp: Jacob & Hallmark, 1996; profile from recent raised field sediments, Pulltrouser Swamp: Wiseman, 1983; Twin Cays: Wooller et al., 2004), changes may

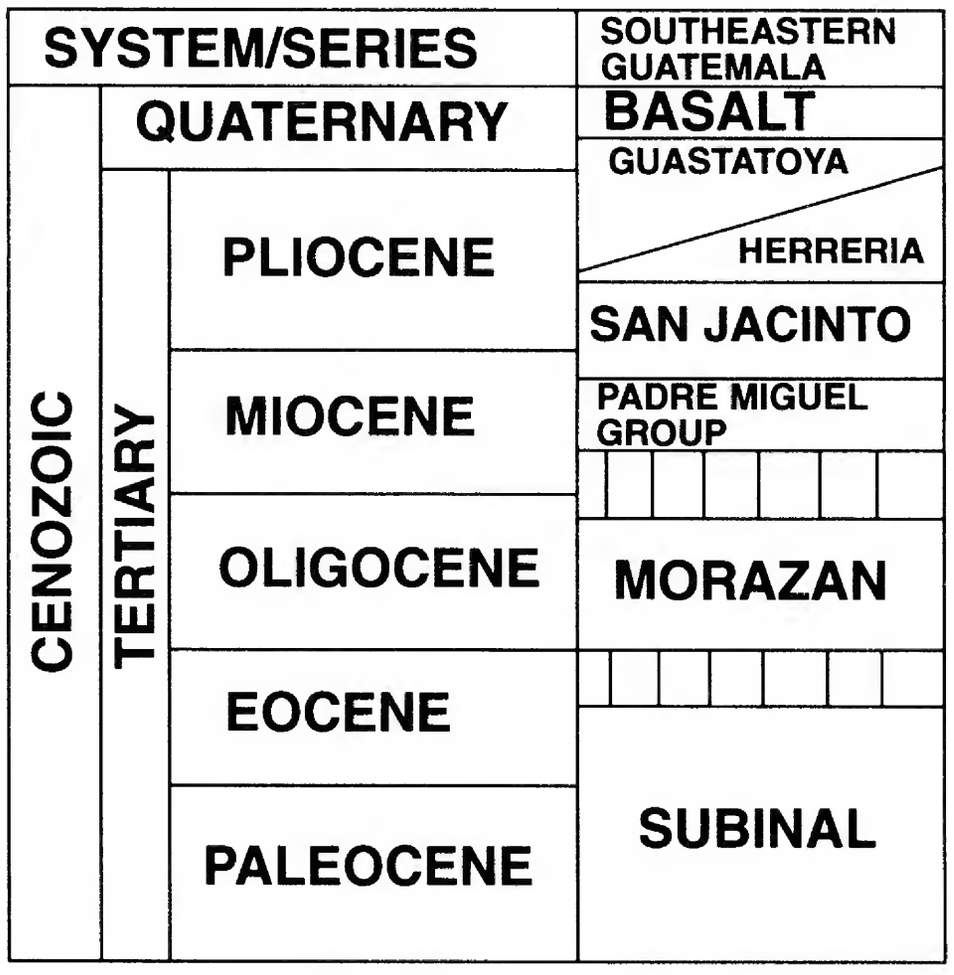


Figure 6.5. Generalized stratigraphic column for Tertiary strata in southeastern Guatemala. Based on Donnelly et al. (1990), courtesy of Geological Society of America.

Table 6.1. Plant fossils from the Late Cretaceous and Cenozoic of Central America. Unless otherwise indicated, spellings, suggested biological affinities, and age assignments are according to the original authors. Unknowns and specimens designated by an informally applied artificial nomenclature are not included. Unpublished studies are cited in the References but are not included in the table. Fungal spores and reproductive structures (e.g., cleistothecia), Pyrrophyta (dinoflagellates), and other algae (including diatoms) are often treated in separate publications, and only those cited in the references below are included here. Refs. = references, as follows, Late Cretaceous: 1 = Stephenson and Berry 1929; Eocene: 2 = Graham 1985; Miocene: 3 = Berry 1921b, 4 = Berry 1928, 5 = Berry 1921a, 6 = Berry 1918; early Miocene: 7 = Graham 1988a, 8 = Graham 1988b, 9 = Graham 1989; late Miocene: 10 = Graham 1991a, b, c, 11 = Graham 1998; Pliocene: 12 = Graham 1998, 13 = Graham 1987a, 14 = Graham and Dilcher 1998; Plio–Pleistocene: 15 = Lötschert and Mädler 1975. Occurrences and references for the Quaternary are listed separately at the end of the table.

Late Cretaceous (99–65 Ma)

Megafossils

[1, Chipaxché Ranch, District Verapaz, Guatemala, no formation, Late Cretaceous (?)]

Ferns and allied groups: *Dicksoniopsis conipteroides*; gymnosperm: *Araucarites*

Late Eocene (37–33.7 Ma)

Microfossils

[2, Gatuncillo Formation, Alcalde Díaz (Boyd-Roosevelt Highway), Panama]

Ferns and allied groups: *Ceratopteris* (Pteridaceae), monolete fern spores (5 types), *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae), *Sphaeropteris–Trichipteris* (Cyatheaceae), trilete fern spores (5 types). Angiosperms (monocotyledons): cf. *Tillandsia* (2 types; Bromeliaceae), Palmae (5 types). Angiosperms (dicotyledons): *Alfaroa–Engelhardia* [*Oreomunnea*; Juglandaceae], cf. Araliaceae, cf. *Campnosperma* (Anacardiaceae), *Cardiospermum* (Sapindaceae), *Casearia* (Flacourtiaceae), cf. *Chrysophyllum* (Sapotaceae), *Coccoloba* (Polygonaceae), *Combretum–Terminalia* (Combretaceae), *Crudia* (Leguminosae), *Eugenia–Myrcia* (Myrtaceae), *Faramea* (2 types; Rubiaceae), cf. *Ficus* (Moraceae), *Ilex* (Aquifoliaceae), *Lisianthius* (Gentianaceae), Malpighiaceae (2 types), *Mortoniodendron* (Tiliaceae), *Paragonia–Arrabidaea* (Bignoniaceae), *Paullinia* (Sapindaceae), *Pelliceria* (Pelliceriaceae), *Protium* (Burseraceae), *Rhizophora* (Rhizophoraceae), *Sabicea* (Rubiaceae), *Serjania* (Sapindaceae), *Tetragastris* (Burseraceae), cf. *Tontelea* (Celastraceae), (+ 40 unknown types)

Miocene (23.8–5.3 Ma), Mio–Pliocene (~5.3 Ma)

Neogene unspecified

Megafossils

[3, Gatún Formation, (middle to late Miocene, see below), Canal Zone, Panama]

Angiosperm (monocotyledon): *Iriartites vaughani* (Palmae)

[4, Uscari (Río Banano, Pliocene, see below) Formation, Province of Chiriquí, Panama]

Angiosperm (monocotyledon): *Palmocarpon geonomoides* (Palmae)

[5, Río Banano Formation, (Pliocene, see below), Sheroli Creek (Sixaola), Talamanca Valley, Costa Rica; see text for other fossils of Tertiary age, private collections, etc.]

An(n)ona costaricana (Annonaceae), *Bü(y)ttneria cinnamomifolia* (Sterculiaceae), *Ficus talamancana* (Moraceae), *Goeppertia tertiaria* (Lauraceae), *Heliconia* (Heliconiaceae), *Hieronymia lehmanni* (Euphorbiaceae), *Inga sheroliensis* (Leguminosae), *Nectandra areolata*, *N. woodringi* (Lauraceae), *Piperites cordatus*, *P. quinquecostatus* (Piperaceae). Incertae sedis: *Phyllites costaricensis*

[6, various formations, Miocene, several localities, Canal Zone, Panama]

Ferns and allied groups: *Acrostichum* (Pteridaceae). Angiosperm (monocotyledon): *Palmoxylon palmacites* (Palmae). Angiosperms (dicotyledons): *Banisteria praenuntia* (Malpighiaceae), *Calyptranthes gatunensis* (Myrtaceae), *Cassia culebrensis* (Leguminosae), *Diospyros macdonaldi* (Ebenaceae), *Ficus culebrensis* (Moraceae), *Guatteria culebrensis* (Annonaceae), *Hieronymia lehmanni* (Euphorbiaceae), *Hiraea oligocaenica* (Malpighiaceae), *Inga oligocaenica* (Leguminosae), *Melastomites miconioides* (Melastomataceae), *Mespilodaphne culebrensis* (Lauraceae), *Myristicophyllum panamense* (Myristicaceae), *Rondeletia goldmani* (Rubiaceae), *Rubiacites ixoreoides* (Rubiaceae), *Schmidelia bejucensis* (Sapindaceae), *Taenioxylon multiradiatum* (Leguminosae)

Microfossils

[7, Culebra Formation, early Miocene, former Canal Zone, Panama]

Ferns and allied groups: cf. *Acrostichum* (Pteridaceae)–*Antrophyum* (Vittariaceae), *Cyathea* (Cyatheaceae), *Danaea* (Marattiaceae), *Lycopodium* (Lycopodiaceae), *Lygodium* (Schizaeaceae), monolete fern spores (3 types), *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae), trilete fern spores (4 types). Angiosperms (monocotyledons): cf. *Dioscorea–Rajania* (Dioscoreaceae), Gramineae, Palmae–*Cryosophila* type, *Desmoncus* type, *Manicaria* type, *Synechanthus* type. Angiosperms (dicotyledons): *Acacia* (Leguminosae), *Alchornea* (Euphorbiaceae), *Allophylus* (Sapindaceae), *Casearea* (Flacourtiaceae), chenoams, *Combretum–Terminalia* (Combretaceae), Compositae, *Cupania* (Sapindaceae), *Doliocarpus* (Dilleniaceae), *Eugenia–Myrcia* (Myrtaceae), cf. *Guazuma* (Sterculiaceae), *Hampea–Hibiscus* (Malvaceae), *Ilex* (Aquifoliaceae), Malpighiaceae, *Matayba* (Sapindaceae), cf. *Pouteria* (Sapotaceae), *Rhizophora* (Rhizophoraceae), cf. *Rourea* (Connaraceae), *Sabicea* (Rubiaceae), *Sapium* (Euphorbiaceae), *Tetrorchidium* (Euphorbiaceae), (+ 14 unknown types)

[8, Cucaracha Formation, early Miocene, former Canal Zone, Panama]

Ferns and allied groups: cf. *Acrostichum* (Pteridaceae)–*Antrophyum* (Vittariaceae), *Ceratopteris* (Pteridaceae), *Cyathea* (Cyatheaceae), monolete fern spores (3 types), *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae), trilete fern spores (2 types). Angiosperms (monocotyledons): Palmae–*Cryosophila* type, *Manicaria* type. Angiosperms (dicotyledons): *Alchornea* (Euphorbiaceae), *Alfaroa–Engelhardia* [*Oreomunnea*; Juglandaceae], Compositae, *Crudia* (Leguminosae), *Eugenia–Myrcia* (Myrtaceae), *Ilex* (Aquifoliaceae), *Rhizophora* (Rhizophoraceae), (+ 2 unknown types)

[9, La Boca Formation, early Miocene, former Canal Zone, Panama]

Fungi: Ascomycete cleistothecium. Algae (Pyrrophyta, dinoflagellates): *Operculodinium centrocarpus*, *Spiniferites*. Ferns and allied groups: cf. *Acrostichum* (Pteridaceae)–*Antrophyum* (Vittariaceae), *Cyathea* (Cyatheaceae), *Lycopodium* (Lycopodiaceae), monolete fern spores (5 types), *Pteris* (2 types; Pteridaceae), *Selaginella* (Selaginellaceae), trilete fern spores (3 types). Angiosperms (monocotyledons): Gramineae, Palmae–*Attalea* type, *Manicaria* type, *Synechanthus* type. Angiosperms (dicotyledons): cf. *Aguiaria* (Bombacaceae), *Alchornea* (Euphorbiaceae), *Alfaroa–Engelhardia* [–*Oreomunnea*] (Juglandaceae), cf. *Ceiba* (Bombacaceae), *Crudia* (Leguminosae), *Ilex* (Aquifoliaceae), Malpighiaceae (5 types), Malvaceae, *Pelliceria* (Pelliceriaceae), *Pseudobombax* (Bombacaceae), *Rhizophora* (Rhizophoraceae), Rubiaceae (2 types), *Utricularia* (Lentibulariaceae), (+ 15 unknown types)

[10, Gatún Formation, late Miocene, former Canal Zone, Panama]

Algae (Pyrrophyta, dinoflagellates undifferentiated). Ferns and allied groups: *Alsophila* (Cyatheaceae), *Ceratopteris* (Pteridaceae), *Cnemidaria* (Cyatheaceae), *Ctenitis* (3 types; Dryopteridaceae), *Cyathea* (2 types; Cyatheaceae), *Grammitis* (Polypodiaceae), *Lycopodium* (4 types; Lycopodiaceae),

Table 6.1. Plant fossils from the Late Cretaceous and Cenozoic of Central America. *(Continued)*

monolete fern spores (5 types), *Ophioglossum* (Ophioglossaceae), *Pteris* (5 types; Pteridaceae), *Selaginella* (Selaginellaceae), trilete fern spores (2 types). Gymnosperms: *Podocarpus* (Podocarpaceae). Angiosperms (monocotyledons): Gramineae, Palmae (2 types). Angiosperms (dicotyledons): *Acacia* (Leguminosae), *Aegiphila* (Verbenaceae), cf. *Aguiaria* (Bombacaceae), *Alchornia* (Euphorbiaceae), *Alfaroa–Oreomunnea* (Juglandaceae), *Allophylus* (Sapindaceae), *Bernoulia* (Bombacaceae), cf. *Bucida* (Combretaceae), cf. *Bumelia* (Sapotaceae), *Bursera* (Burseraceae), *Cabomba* (Cabombaceae), *Casimiroa* (Rutaceae), *Cedrela* (Meliaceae), *Ceiba* (Bombacaceae), *Chomelia* type (Rubiaceae), cf. *Cionosicys* (Cucurbitaceae), *Combretum–Terminalia* (Combretaceae), Compositae (Mutisieae type), *Cosmibuena* (Rubiaceae), *Crudia* (Leguminosae), *Cupania* (Sapindaceae), *Cymbopetalum* (Annonaceae), Ericaceae (2 types), *Erythrina* (Leguminosae), *Eugenia–Myrcia* (Myrtaceae), *Faramea* (2 types; Rubiaceae), cf. *Glycydendron* (Euphorbiaceae), *Guarea* (Meliaceae), *Hampea–Hibiscus* (Malvaceae), *Hauya* (Onagraceae), *Ilex* (Aquifoliaceae), cf. *Jatropha* (Euphorbiaceae), Loranthaceae (2 types), Malpighiaceae (2 types), Melastomataceae, *Mortoniodendron* (Tiliaceae), *Paullinia* (Sapindaceae), *Petrea* (Verbenaceae), *Posoqueria* (Rubiaceae), *Pseudobombax* (Bombacaceae), *Quercus* (Fagaceae), *Rhizophora* (Rhizophoraceae), *Serjania* (Sapindaceae), cf. *Stillingia* (Euphorbiaceae), *Symplocos* (Symplocaceae), *Utricularia* (*Lentibulariaceae*), (+ 27 unknown types)

[11, Padre Miguel Formation, Mio–Pliocene, east-central Guatemala]

Algae (Pyrrophyta, dinoflagellates): *Operculodinium*. Ferns and allied groups: *Lycopodium* (Lycopodiaceae), *Selaginella* (Selaginellaceae). Gymnosperms: *Picea* (Pinaceae), *Pinus* (Pinaceae). Angiosperms (monocotyledons): Cyperaceae, Gramineae, Palmae. Angiosperms (dicotyledons): *Alfaroa–Oreomunnea* (Juglandaceae), Compositae, *Iresine* (Amaranthaceae), *Juglans* (Juglandaceae), *Ludwigia* (Onagraceae), *Quercus* (Fagaceae), *Ulmus* (Ulmaceae)

Pliocene (5.3–2.6 Ma)

Microfossils

[12, Herrería Formation, Pliocene, southeastern Guatemala]

Algae (Pyrrophyta, dinoflagellates): *Operculodinium*. Ferns and allied groups: cf. *Acrostichum* (Pteridaceae), cf. *Antrophyum* (Vittariaceae), *Selaginella* (Selaginellaceae). Gymnosperms: *Pinus* (Pinaceae). Angiosperms (monocotyledons): Cyperaceae, Gramineae, Palmae. Angiosperms (dicotyledons): *Alfaroa–Oreomunnea* (Juglandaceae), *Caesalpinia* (Leguminosae), Compositae, *Rhizophora* (Rhizophoraceae), *Ulmus* (Ulmaceae)

[13, Río Banano Formation, Pliocene, Sheroli Creek (Sixaola), Costa Rica]

Fungi (Ascomycetes): *Microthyrium* type. Bryophyta (Anthrocerotaceae): *Phaeoceros*, Muscae. Ferns and allied groups: *Cnemidaria* (Cyatheaceae), cf. *Hymenophyllum* (Hymenophyllaceae), *Lophosoria* (Lophosoriaceae), *Lycopodium* (Lycopodiaceae), *Pityrogramma* (Pteridaceae), *Pteris* (Pteridaceae), *Selaginella* (Selaginellaceae). Gymnosperm: *Podocarpus* (Podocarpaceae). Angiosperms (dicotyledons): *Alchornea* (Euphorbiaceae), cf. *Banisteriopsis* (Malpighiaceae), Bombacaceae, Compositae, Ericaceae, *Eugenia–Myrcia* (Myrtaceae), cf. *Glycydendron* (Euphorbiaceae), cf. *Hiraea* (Meliaceae), *Ilex* (Aquifoliaceae), *Lisianthius* (Gentianaceae), Melastomataceae, *Rhizophora* (Rhizophoraceae)

[14, Río Banano Formation, Pliocene, Zent, Costa Rica]

Ferns and allied groups: cf. *Antrophyum* (Vittariaceae), *Pteris* (Pteridaceae). Angiosperms (monocotyledon): Palmae. Angiosperms (dicotyledons): *Alchornea* (Euphorbiaceae), *Ilex* (Aquifoliaceae), *Lacmellea* (Apocynaceae), *Pelliceria* (Pelliceriaceae), Polygonaceae, cf. *Psittacanthus* (Loranthaceae), *Sabicea* (Rubiaceae), cf. *Struthanthus* (Loranthaceae), *Symphonia* (Guttiferae)

Plio–Pleistocene

[15, Sisimico–Tal, Cuscatlán sequence, Río Sisimico Valley, El Salvador]

Megafossils

Ferns and allied groups: cf. *Acrostichum* (Pteridaceae), *Adiantum* (Pteridaceae), *Ceratopteris* (Pteridaceae), *Equisetum* (Equisetaceae), *Isoetes* (Isoetaceae), *Polypodium* (Polypodiaceae), cf. *Rhipidopteris–Elaphoglossum* (Dryopteridaceae), *Salvinia* (Salviniaceae). Gymnosperms: *Abies*, *Picea*. Angiosperms (monocotyledons): Gramineae, Gramineae–Cyperaceae, Palmae, cf. *Potamogeton* (Potamogetonaceae). Angiosperms (dicotyledons): cf. *Acacia* (Leguminosae), cf. *Acridocarpus* (Malpighiaceae), *An(n)ona* (Annonaceae), *Banisteria* (Malpighiaceae), *Bauhinia* (Leguminosae), Bignoniaceae, *Bucida buceras* (Combretaceae), *Cedrela* (Meliaceae), *Ceratophyllum demersum*, cf. *C. llerenae* (Ceratophyllaceae), cf. *Copaifera* (Leguminosae), cf. *Cotinus coggygria* (Anacardiaceae), cf. *Enterolobium* (Leguminosae), *Eugenia* (Myrtaceae), *Ficus*, cf. *F. cotinifolius* (Moraceae), cf. *Haematoxylon* (Leguminosae), cf. *Hamamelis* (Hamamelidaceae), cf. *Hippuris* (Hippuridaceae), cf. *Hiraea* (Malpighiaceae), cf. *Ilex* (Aquifoliaceae), cf. *Inga* (Leguminosae), cf. *Karwinskia* (Rhamnaceae), *Marsdenia macrophylla* (Asclepidaceae), cf. *Myrica* (Myricaceae), *Myroxylon* cf. *balsamum* (Leguminosae), cf. *Ocotea* (Lauraceae), cf. *Peperomia* (Piperaceae), cf. *Persea* (Lauraceae), cf. *Pithecolobium* (Leguminosae), cf. *Psidium* (Myrtaceae), cf. *Pterocarpus* (Leguminosae), *Quercus*, cf. *Q. crassifolia* (Fagaceae), cf. *Rhus* (Anacardiaceae), cf. *Salix* (Salicaceae), cf. *Strychnos* (Strychnaceae), cf. *Symplocos limoncillo*, cf. *Symplocos* (Symplocaceae)

Microfossils

Ferns and allied groups: Polypodiaceae. Gymnosperms: cf. *Abies* (Pinaceae), *Pinus* (Pinaceae). Angiosperms (monocotyledons): Cyperaceae, Gramineae. Angiosperms (dicotyledons): *Carya* (Juglandaceae), cf. *Ceiba* (Bombacaceae), cf. *Celtis* (Ulmaceae), Chenopodiaceae [chenoam], Compositae, cf. *Ficus* (Moraceae), *Juglans* (Juglandaceae), cf. Melastomataceae, Myrtaceae, Polygonaceae, cf. *Pterocarya* (Juglandaceae [Asian; possibly if Pliocene]), *Quercus* (Fagaceae), cf. Sapotaceae, *Ulmus* type (Ulmaceae)

Quaternary (~2.6 Ma–Present)

Guatemala: 1 = Lake Salpeten, Leyden 2002; 2 = Lake Petén Itzá, Islebe et al. 1996b; 3 = Laguna de Petenxil, Tsukada 1966 (pollen); 4 = Laguna de Petenxil (other plant microfossils), Hutchinson and Goulden 1966; 5 = Lake Izabal, Tsukada and Deevey 1967; 6 = Lake Amatitlán, Tsukada and Deevey 1967; 7 = Lake Quexil, Leyden 2002 (see also Leyden et al. 1994, Mexico); 8 = Laguna Tamarindito, Dunning et al. 1998. Belize: 9 = Lake Coba, Leyden 2002; 10 = Lake Chichancanab, Leyden 2002; 11 = Laguna de Cocos, Hansen 1990; 12 = Pulltrouser Swamp, Wiseman 1983 (raised field, most very recent). El Salvador: 13 = Lake Guija, Tsukada and Deevey 1967; 14 = Lake Cuscachapa, Tsukada and Deevey 1967. Costa Rica: 15 = Lachner Bog, Martin 1961; 16 = La Chonta, Islebe and Hooghiemstra 1997; 17 = Río General, Kesel 1983. Panama: 18 = Gatún, Bartlett and Barghoorn 1973; 19 = El Valle, Bush and Colinvaux 1990; 20 = Lake La Yeguada, Bush et al. 1992 (20a = taxa reported as phytoliths); 21 = Lake Wodehouse, Bush and Colinvaux 1994; 22 = Cana Swamp, Bush and Colinvaux 1994; 23 = Changuinola Swamp, Phillips et al. 1997.

Fungi (spores):	2, 8, 16
Algae:	
Botryococcus	2, 4, 8, 16
Gloeocapsa	8
Micrasterias	4
Pediastrum	2, 4
Staurastrum	4
Ferns and allied groups:	
Isoetes (Isoetaceae)	15, 16
Lycopodium (Lycopodiaceae)	15, 16, 18
Selaginella (Selaginellaceae)	18, 23
Acrostichum (Pteridaceae)	18, 23
Blechnum (Blechnaceae)	16
Cyatheaceae	16, 19
Danaea type (Marattiaceae)	18
Dryopteris type (Dryopteridaceae)	11
Grammitis (Polypodiaceae)	16

Table 6.1. Plant fossils from the Late Cretaceous and Cenozoic of Central America. *(Continued)*

Hemitelia (Cyatheaceae)	18
Hymenophyllum (Hymenophyllaceae)	16
Jamesonia (Pteridaceae)	16
Lophosoria (Lophosoriaceae)	16
Ophioglossum (Ophioglossaceae)	16
Osmunda type (Osmundaceae)	11
Polypodiaceae	19
Pteridium type (Dennstaedtiaceae)	11
Trichomanes (Hymenophyllaceae)	20a
Gymnosperms:	
Cupressaceae	11
Ephedra (Ephedraceae)	11
Juniperus (Cupressaceae)	1
Pinus (Pinaceae)	1, 2, 3, 5, 6, 7, 8, 11, 12, 13, 14, 17
Podocarpus (Podocarpaceae)	2, 3, 5, 6, 11, 13, 14, 15, 16, 17, 18
Angiosperms (monocotyledons):	
Agave (Agavaceae)	11
Allium type (Liliaceae)	11
Chusquea (Gramineae)	20a
Cyperaceae	1, 2, 3, 6, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 20a, 21, 22, 23
Cyperus/Kyllinga (Cyperaceae)	20a
Euchlaena (Gramineae)	3
Euterpe (Palmae)	23
Gramineae–Poaceae	1, 2, 3, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23
Iriartea (Palmae)	18
Limnocharis (Limnochariaceae)	19, 20
Palmae	2, 3, 5, 9, 11, 17, 18, 20a, 22, 23
Phytelephas (Palmae)	18
Pontederiaceae	18
Potamogeton (Potamogetonaceae)	3
Puya (Bromeliaceae)	16
Raphia (Palmae)	23
Sparganium type (Sparganiaceae)	11
Typha (Typhaceae)	1, 2, 3, 8, 18, 19, 21
Zea, *Z. mays* (Gramineae)	1, 2, 3, 6, 8, 9, 10, 11, 12, 13, 18, 21, 22
Angiosperms (dicotyledons):	
Acacia (Leguminosae)	3, 12, 17
Acalypha (Euphorbiaceae)	1, 2, 9, 10, 11, 17, 18, 21, 22
Acer (Aceraceae)	11
Achras (Sapotaceae)	3
Alchornea (Euphorbiaceae)	2, 5, 6, 11, 14, 16, 17, 18, 22
Alfaroa–Oreomunnea (Juglandaceae)	15
Alnus (Betulaceae)	2, 3, 5, 6, 11, 13, 14, 15, 16, 17, 18
Alternanthera *Alternanthera* type (11) (Amaranthaceae)	1, 11, 19, 20
Ambrosia type (Compositae)	1, 2, 3, 11
Anacardiaceae	2, 9, 11, 18
Annonaceae	17, 18
Antidaphne (Loranthaceae)	16
Apeiba (Tiliaceae)	18
Aphelandra (Acanthaceae)	18
Apocynaceae	18
Araliaceae	6, 13, 14
Asteraceae Tubuliflorae (11, 19); 6, 13, 14 includes *Ambrosia*; high-spine, 12, 17 includes low-spine	1, 2, 3, 6, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 20a, 22
Avicennia (Avicenniaceae)	18
Bauhinia emarginata (Leguminosae)	18
Bocconia (Papaveraceae)	11, 16
Bombacaceae	2, 11, 12, 17
Bombax (Bombacaceae)	3
Borreria (Rubiaceae)	11, 18
Brassicaceae (see Cruciferae)	
Brosimum, *Brosimum* type (11) (Moraceae)	1, 9, 10, 11
Bue(y)ttneria (Sterculiaceae)	18
Bursera (Burseraceae)	1, 3, 5, 6, 9, 10, 11, 12, 13, 14, 18, 20
Burseraceae	2, 8
Byrsonima	1, 2, 9, 11, 17, 18, 19, 20
B. crassifolia (Malpighiaceae)	17
Calliandra (Leguminosae)	17, 18
Campnosperma (Anacardiaceae)	23
Canavalia (Leguminosae)	18
Carpinus, *Carpinus* type (Betulaceae)	2, 3, 11
Caryophyllaceae	3, 9, 11, 16, 20
Cassipourea (Rhizophoraceae)	18
Catopsis (Bombacaceae)	18
Cavanillesia (Bombacaceae)	18
Cecropia (Urticaceae)	1, 2, 9, 11, 16, 19, 20, 21, 22
Ceiba (Bombacaceae)	11, 13, 14, 18
Celastraceae type	11

Table 6.1. Plant fossils from the Late Cretaceous and Cenozoic of Central America. *(Continued)*

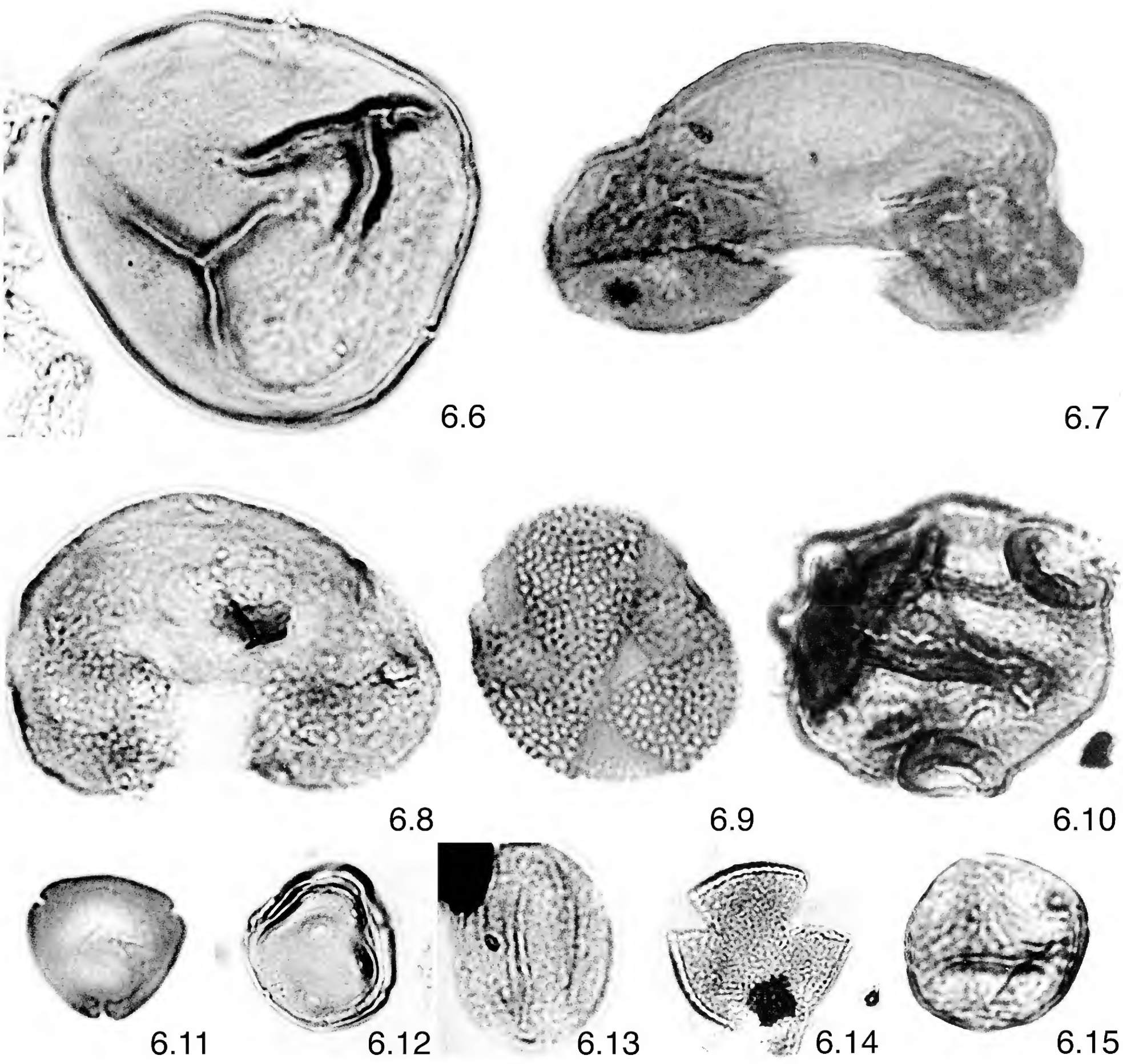
Celtis (Ulmaceae)	1, 2, 3, 6, 9, 10, 11, 12, 13, 14, 17
Chaetoptelea (Ulmaceae)	3, 5, 6, 9, 13, 14
Chenoam	1, 2, 3, 6, 7, 9, 10, 11, 12, 13, 14, 17, 18, 19, 22
Chlorophora (Moraceae)	1
Chrysobalanaceae	20a
Cissus (Vitaceae)	18
Citrus type (Rutaceae)	3
Cleome (Capparidaceae)	16
Clethra (Clethraceae)	16
Clusia (Guttiferae)	16
Coccoloba *Coccoloba* type (18) (Polygonaceae)	3, 11, 12, 18
Combretaceae–Melastomataceae	11
Combretum (Combretaceae)	18
Combretum–Terminalia (Combretaceae)	8
Compsoneura (Myristicaceae)	18
Conocarpus (Combretaceae)	18
Copaifera (Leguminosae)	18
Corchorus (Tiliaceae)	11
Cordia alliodora (Boraginaceae)	18
Couroupita (Lecythidaceae)	18
Cruciferae	11, 16
Cupania (Sapindaceae)	18
Cupuliferoidae (Fagales, fagaceous)	8
Cyrilla (Cyrillaceae)	23
Dialyanthera (Myristicaceae)	18
Dodonea arborea (Sapindaceae)	11
Drepanocarpus type (Leguminosae)	18
Drimys (Winteraceae)	15, 16
Echinocereus (Cactaceae)	11
Ericaceae	15, 16, 17, 18
Eriocaulaceae	16
Erythrina	17, 18
E. glauca (Leguminosae)	18
Eugenia (Myrtaceae)	3
Euphorbiaceae	2, 11, 16
Crotonoid	18
Faramea (Rubiaceae)	18
Ficus (Moraceae)	11
Flacourtiaceae	2
Gaiadendron (Loranthaceae)	16
Gentiana cf. *crinita* (Gentianaceae)	11
Gentianaceae	16
Geranium (Geraniaceae)	11
Glycydendron (Euphorbiaceae)	18
Gossypium (Malvaceae)	12
Guatteria type (Annonaceae)	20a
Gunnera (Haloragidaceae)	16
Gyranthera darienensis type (Bombacaceae)	18
Haematoxylon (Leguminosae)	3
Hedyosmum (Chloranthaceae)	2, 5, 6, 11, 13, 14, 16, 18, 19
Heliconia (Heliconiaceae)	20a
Heliocarpus (Tiliaceae)	6, 13, 14
Hieronyma (Euphorbiaceae)	18
Hippocratea	17
H. volubilis (Celastraceae)	18
Hura (Euphorbiaceae)	19
Hydrangea (Hydrangeaceae)	18
Hypericum (Gutifferae)	16
Ilex (Aquifoliaceae)	3, 16, 17, 18, 20, 23
Ipomoea (Convolvulaceae)	18
Iresine	2, 9, 11, 18
Iva type (Compositae)	11
Juglans (Juglandaceae)	11
Jussiaea (Onagraceae)	18
Justicia (Acanthaceae)	18
Lafoensia (Lythraceae)	18
Leguminosae (see Mimosaceae)	
Leucaena multicapitula (Leguminosae)	18
Licania arborea (Chrysobalanaceae)	18
Liquidambar (Hamamelidaceae)	3, 5, 6, 11, 13, 14
Liriosma (Olacaceae)	18
Luehea	3, 11
L. seemannii (Tiliaceae)	18
Lythraceae	11
Mabea (Euphorbiaceae)	18
Magnolia (Magnoliaceae)	20a
Malouetia (Apocynaceae)	18
Malpighiaceae	3, 5, 11, 13, 14, 17, 18

Table 6.1. Plant fossils from the Late Cretaceous and Cenozoic of Central America. *(Continued)*

Malvaceae	11, 18
Manihot (Euphorbiaceae)	18
Maripa (Convolvulaceae)	18
Melastomataceae	1, 7, 10, 16, 17, 18, 19, 20, 21, 22
Melastomataceae–*Terminalia* (2)	
Meliaceae	2, 19
Meliaceae–Sapotaceae	18
Mendoncia (Mendonciaceae)	18
Menispermaceae	18
Merremia (Convolvulaceae)	18
Mimosaceae	11, 18
Mollugo (Aizoaceae)	18
Moraceae–Urticaceae (see also Urticaceae)	2, 3, 5, 6, 8, 11, 12, 13, 14, 17, 19
Mucuna (Leguminosae)	18
Myrantaceae	20a
Myrica (Myricaceae)	2, 3, 11, 12, 16, 17, 18, 19, 23
Myriophyllum (Haloragidaceae)	11
Myrsine (Myrsinaceae)	16
Myrtaceae	2, 3, 11, 16, 18, 19, 20
Nymphaea (Nymphaeaceae)	3, 11, 12
Ochroma (Bombacaceae)	18
Oryctanthus cordifolius (Loranthaceae)	18
Ostrya–Carpinus, *Ostrya type* (Betulaceae)	11
Ouratea guatemalensis (Ochnaceae)	18
Pachria (Bombaceae)	18
Pacourina edulis (Compositae)	18
Paullinea (Sapindaceae)	18
Phyllanthus (Euphorbiaceae)	18
Pilea (Urticaceae)	20, 21, 22
Piperaceae	17, 18, 20, 21, 22
Piscidia (Leguminosae)	10
Podostemaceae	20a
Polygalaceae	18
Polygonaceae	17
Polygonum, *P. bistortoides* type (Polygonaceae)	11, 18
Portulacaceae	18
Proteaceae	11
Protium (Burseraceae)	23
Pseudobombax (Bombacaceae)	18
Pterocarpus officinalis type (Leguminosae)	18
Puya	16
Quararibea (Bombacaceae)	18
Quassia (Simaroubaceae)	18
Quercus (Fagaceae)	1, 2, 3, 5, 6, 7, 8, 11, 12, 13, 14, 16, 17, 19, 20
Randia (Rubiaceae)	18
Ranunculus (Ranunculaceae)	16
Rau(v)wolfia (Apocynaceae)	18
Rhizophora (Rhizophoraceae)	18
Rosaceae	11, 16
Rubiaceae	2, 16, 17, 18
Rumex type (Polygonaceae)	2, 11
Rutaceae	11
Salix (Salicaceae)	11
Sapindaceae	2, 11, 21
Sapium (Euphorbiaceae)	2, 14, 16, 18
Sapotaceae	3, 5, 6, 12, 14, 17, 19
Sebastiania type (Euphorbiaceae)	11
Sechium (Cucurbitaceae)	18
Senecio (Compositae)	12
Solanaceae	2, 11, 16, 17
Solanum (Solanaceae)	3, 6, 12
Spondias (Anacardiaceae)	2, 3, 12
Swartzia, *S. panamensis* type` (Leguminosae)	18
Symphonia (Guttiferae)	18
Symplocos (Symplocaceae)	16, 18
Tabernaemontana (Apocynaceae)	18
Terminalia [*Combretum–Terminalia*] (Combretaceae)	3, 12
Thalictrum (Ranunculaceae)	16
Tiliaceae	11
Trema, *T. floridana* (Ulmaceae)	1, 3, 5, 6, 10, 11, 12, 14, 20, 21, 22 12
Trichanthera (Acanthaceae)	18
Tristicha (Podostemaceae)	18
Trophis (Moraceae)	10
Ulmaceae?	3
Ulmus (Ulmaceae)	11, 16
Umbelliferae	15, 16, 17, 21
Urticaceae	11
Urticaceae–Moraceae	20, 21, 22
Urticales	1, 16, 18
Valeriana (Valerianaceae)	16
Viburnum (Caprifoliaceae)	16

Table 6.1. Plant fossils from the Late Cretaceous and Cenozoic of Central America. *(Continued)*

Virola (Myristicaceae)	18
Vitaceae	11
Vitis (Vitaceae)	3
Vochysia (Vochysiaceae)	18
Weinmannia (Cunoniaceae)	11, 16
Zanthoxylum	3, 17
Z. panamensis?	18
Z. setulosum (Rutaceae)	18
Zuelania (Flacourtiaceae)	3



Figures 6.6–6.15. Plant microfossils from the Neogene Padre Miguel and Herrería floras of Guatemala. 6.6. cf. *Acrostichum* (probably *A. aureum*). 6.7. *Pinus*. 6.8. *Picea*. 6.9. *Caesalpinia*. 6.10. *Ludwigia*. 6.11. *Alfaroa–Oreomunnea*. 6.12. *Juglans*. 6.13, 6.14. Equatorial and polar view of *Quercus*. 6.15. *Ulmus*.

Table 6.2. Numerical representation of palynomorphs in the Padre Miguel Group and Herrería Formation, Guatemala. Figures are percentages based on counts of 200. Dashes indicate presence at <0.5%. Unknowns not included.

Taxon	Padre Miguel Group		Herrería Formation	
	Locality B	Locality 4	Locality F	Locality G
Operculodinium		—		6
Lycopodium	1	2		
Selaginella	1	2	—	2
Monolete fern spore				
Type 1	3	2	16	5
Type 2	4	3	2	4
Type 3	1	—	3	—
Type 4	8	—	1	
cf. *Acrostichum*			45	11
cf. *Anthrophyum*			16	27
Picea	3			
Pinus	3	11	15	2
Cyperaceae	7	29	—	
Gramineae	8	6	—	8
Palmae	4		—	5
Iresine	4			
Compositae	11	9		3
Quercus	12	7		
Alfaroa–Oreomunnea	8	9		3
Juglans	5	2		
Caesalpinia				1
Ludwigia	3			
Rhizophora			~100	
Ulmus	3	3		1

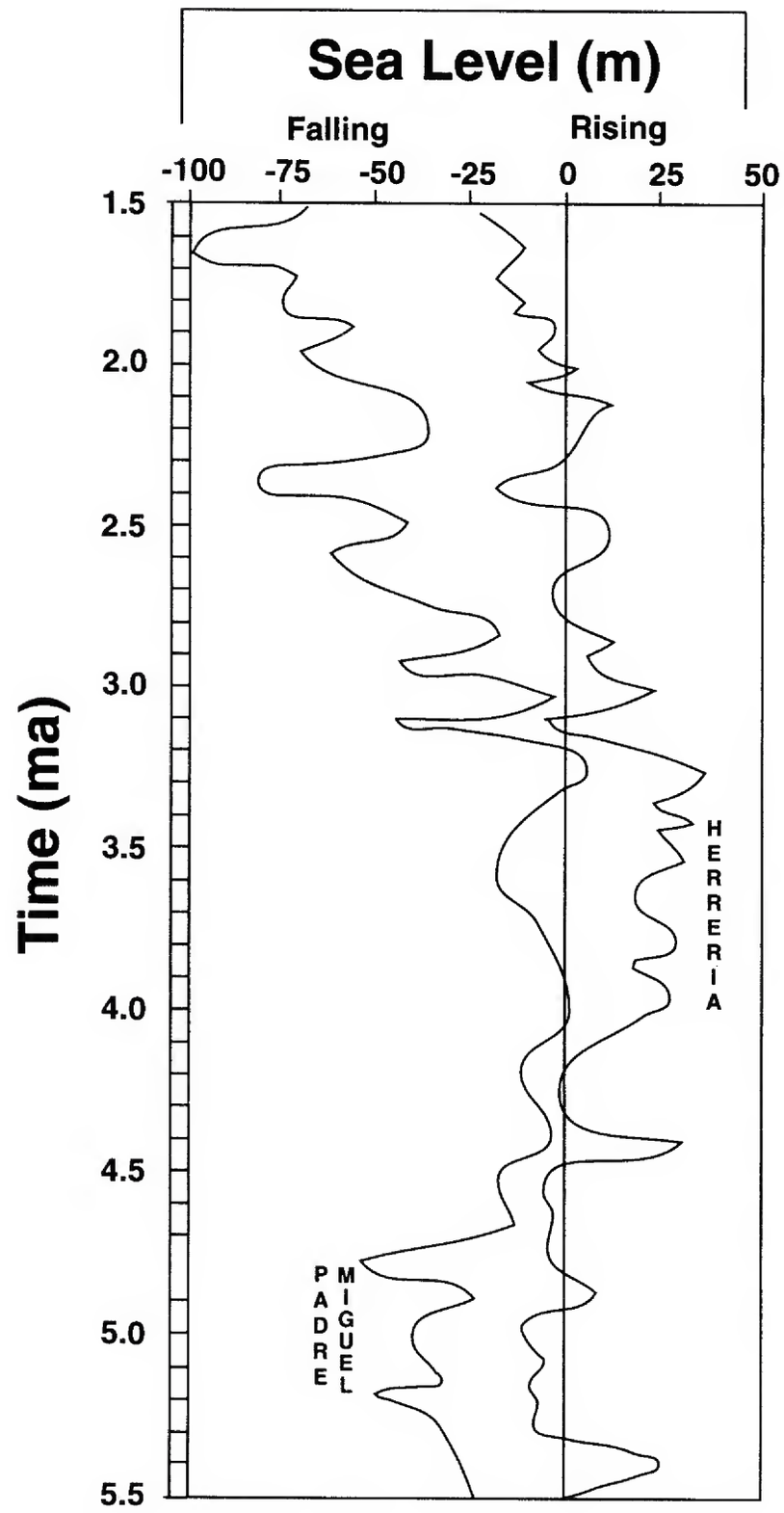


Figure 6.16. Sea-level fluctuations derived from deep-ocean ^{18}O records with inferred age of the Padre Miguel Group and Herrería Formation. The two curves define the range of highstands and lowstands. Based on Krantz (1991), used with permission of Elsevier Science Publishers, Amsterdam.

be compared with those from the basins of central Mexico and the Chihuahuan and Sonoran deserts of northern Mexico (Chapter 4). Interludes of similar climate and vegetation across these regions identify forcing mechanisms that are regional in scope. Similarity between the Petén sequence, central Mexico, and one of the northern regions but not the other, suggests different climate controls operating between the Pacific and Atlantic provinces. If central Mexico is the odd-sequence-out, it suggests intervals when basin tectonics were affecting hydrological patterns. In the following sequence for the Maya lowlands, the bracketed material gives conditions for northern Mexico, and the parenthetical material gives conditions for central Mexico for approximately the same interval.

~36–24 Kyr B.P. (interstadial)—moist but drier than at present, and temperatures cooler by 4.7°–6.5° C; humid to subhumid montane pine-oak forest; *Alfaroa* in moister areas, *Juniperus* in drier areas.

(Central Mexico—humid from at least 34 Kyr B.P. to 23 Kyr B.P.)

~24–12 Kyr B.P. (glacial maximum)—extremely dry, temperatures cooler by 6.5°–8.0° C, lowest lake level; thorn scrub, grasses.

(Central Mexico—dry and cold to ~14 Kyr B.P.)

~12 Kyr B.P. (Late Glacial)—deglaciation, more moist, rising lake levels; temperate oak forest; terrestrial marsh (moist) in Cobweb Swamp, Belize (Jacob & Hallmark, 1996).

[Northern Mexico—Alta Babicora Basin, Chihuahuan Desert, moist, mesic; Cañon de la Fragua and other sites, mesic, beginning a trend toward drying climates]

~12–11 Kyr B.P.—Younger Dryas cooling event (MAT decreases by ~1.5° C).

The record was extended through the Holocene when cores were obtained from Lake Salpeten (Leyden, 1987; Rosenmeier et al., 2002) and from Lake Petén Itzá (Islebe et al., 1996b; Curtis et al., 1998; Anselmetti et al., 2006), and there have been discussions to obtain deep-core Pleistocene sediments from Lake Petén Itzá (Barbara Leyden, pers. comm., 2003). Pollen studies alone do not readily identify climatic trends after the

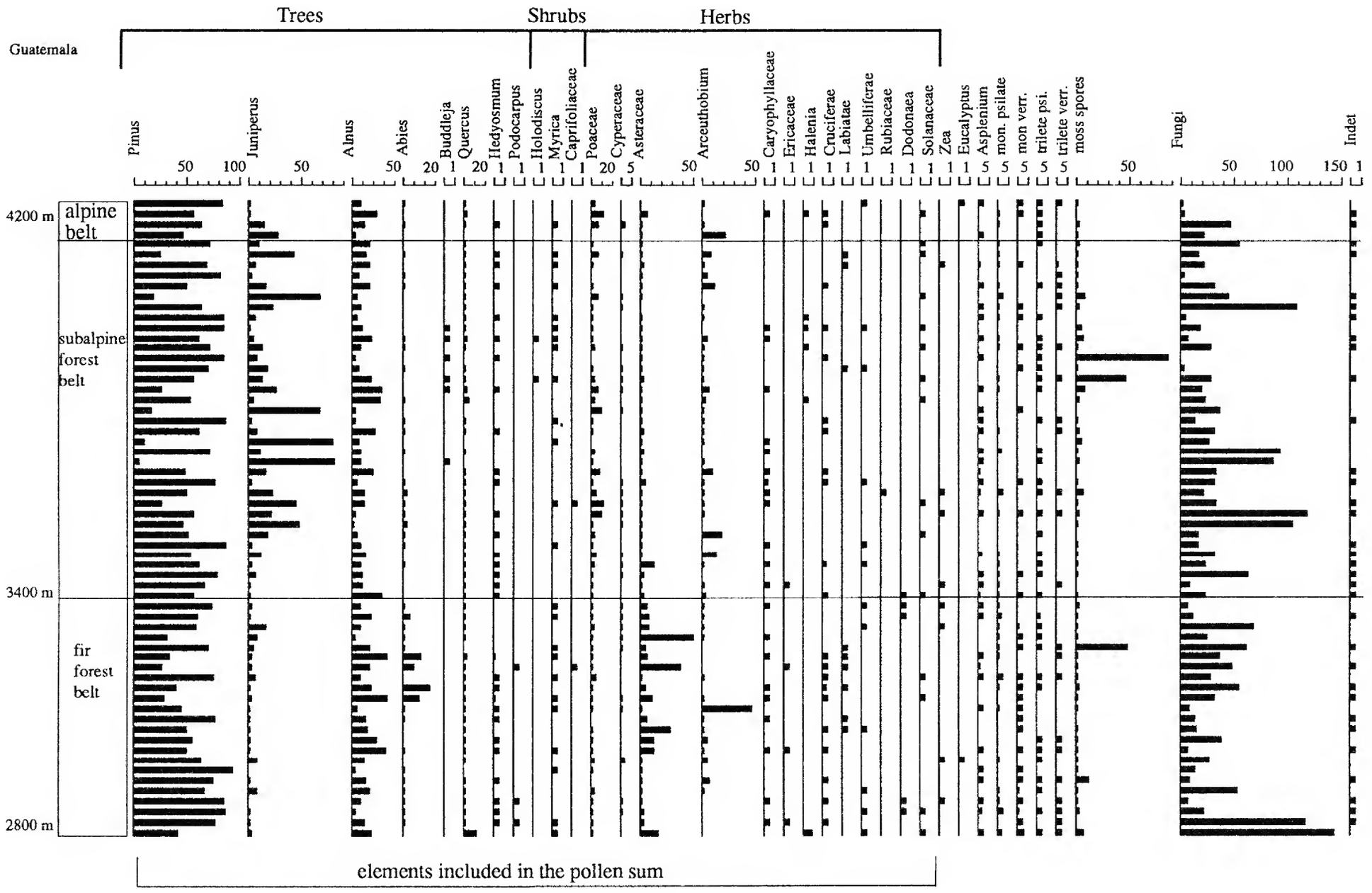


Figure 6.17. Diagram of modern pollen rain percentages in the highlands of Guatemala. From Islebe and Hooghiemstra (1995). Used with permission of Blackwell Scientific Publications, Oxford, U.K.

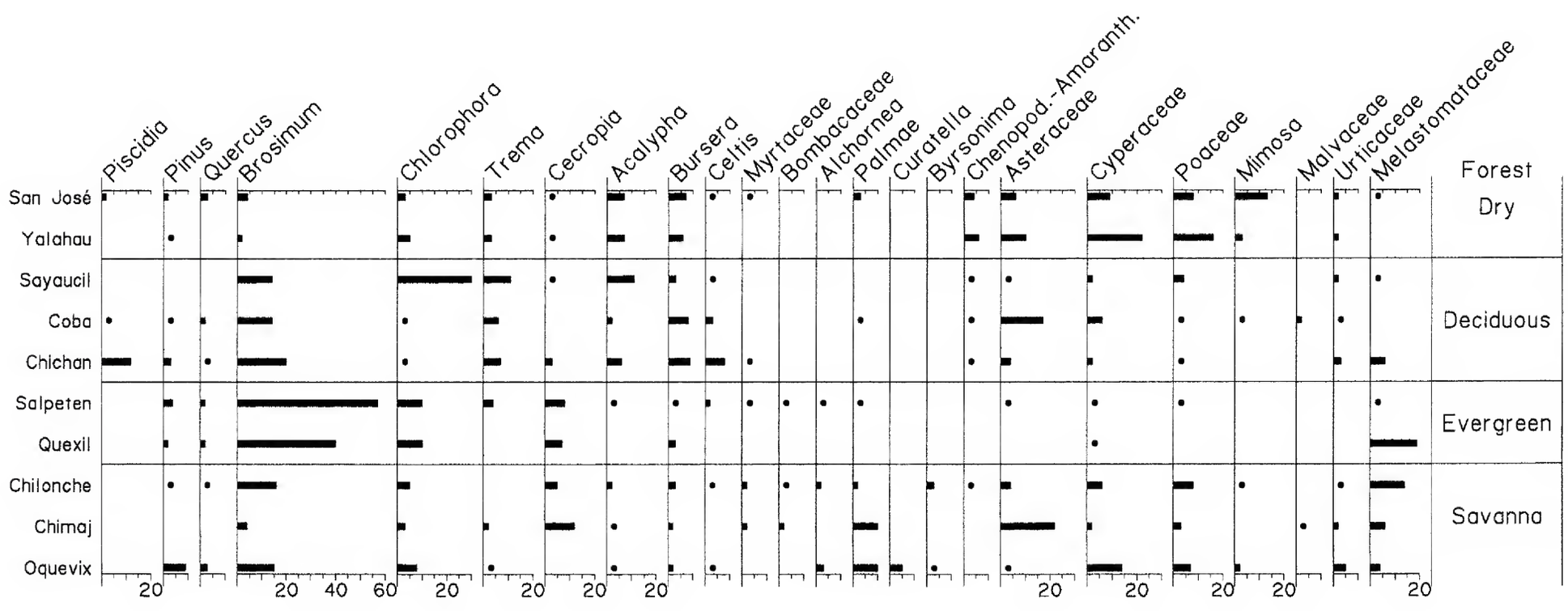


Figure 6.18. Diagram of modern pollen rain percentages in the Maya lowlands of Guatemala. From Leyden (2002). Reprinted with the permission of Cambridge University Press.

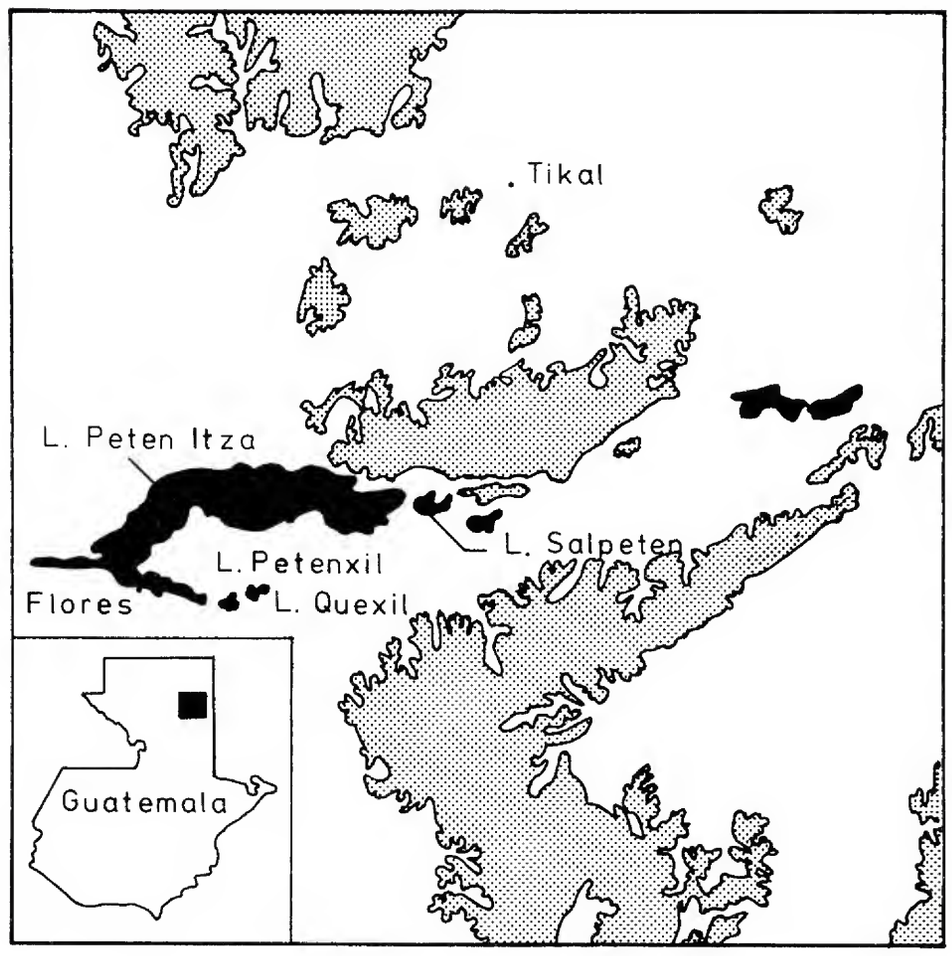


Figure 6.19. Index map of the lake district, Petén, Guatemala. Shaded areas are above 300 m. From Leyden (1984). Used with permission of Bruce J. Cochrane.

Maya population increased in the area, and studies now utilize multi-proxy approaches that allow better differentiation between climatic and human influence on the vegetation. They include sedimentology; ^{210}Pb and AMS (accelerator mass spectrometry) ^{14}C dating; ^{18}O stable isotopes; organic, inorganic carbon, and Ca, Mg, Fe, K, and Na cation composition of sediments; chlorine and sulfate concentration in the lake water, and other lake water and rain water tests; magnetic susceptibility; and palynological evidence. The sequence continues as follows (Curtis et al., 1998; Leyden, 2002):

11–10 Kyr cal. years B.P.—arid toward humid.

>~9000 ^{14}C years B.P. (earliest Holocene)—relatively dry; slope wash into Cobweb Swamp.

[Northern Mexico—wetter and cooler in Sonoran Desert]

~9000 ^{14}C years B.P.—increasing moisture (also in northern part of the Yucatán Peninsula.

(Central Mexico—moist)

~9000–6800 ^{14}C years B.P. (early Holocene)—moist (pollen); relatively high E/P (high ^{18}O), warming.

(Central Mexico—moist)

~6800 ^{14}C years B.P.—wet (change in ostracod species, decrease in ^{18}O), warm, mesic tropical forest (southern lowlands), edaphically dry (northern Yucatán Peninsula).

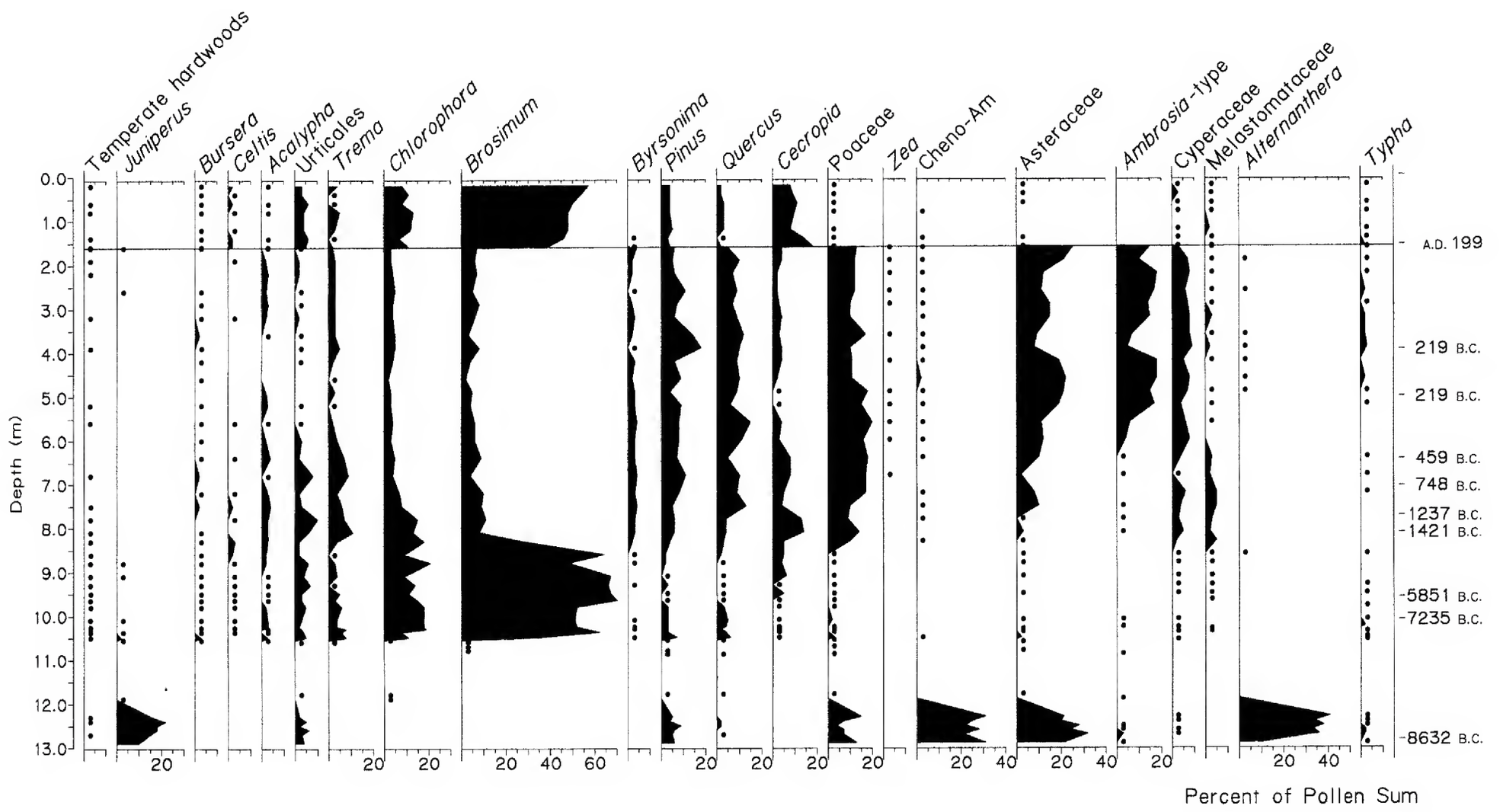


Figure 6.20. Diagram for Lake Salpeten, Petén, Guatemala. From Leyden (2002). Reprinted with the permission of Cambridge University Press.

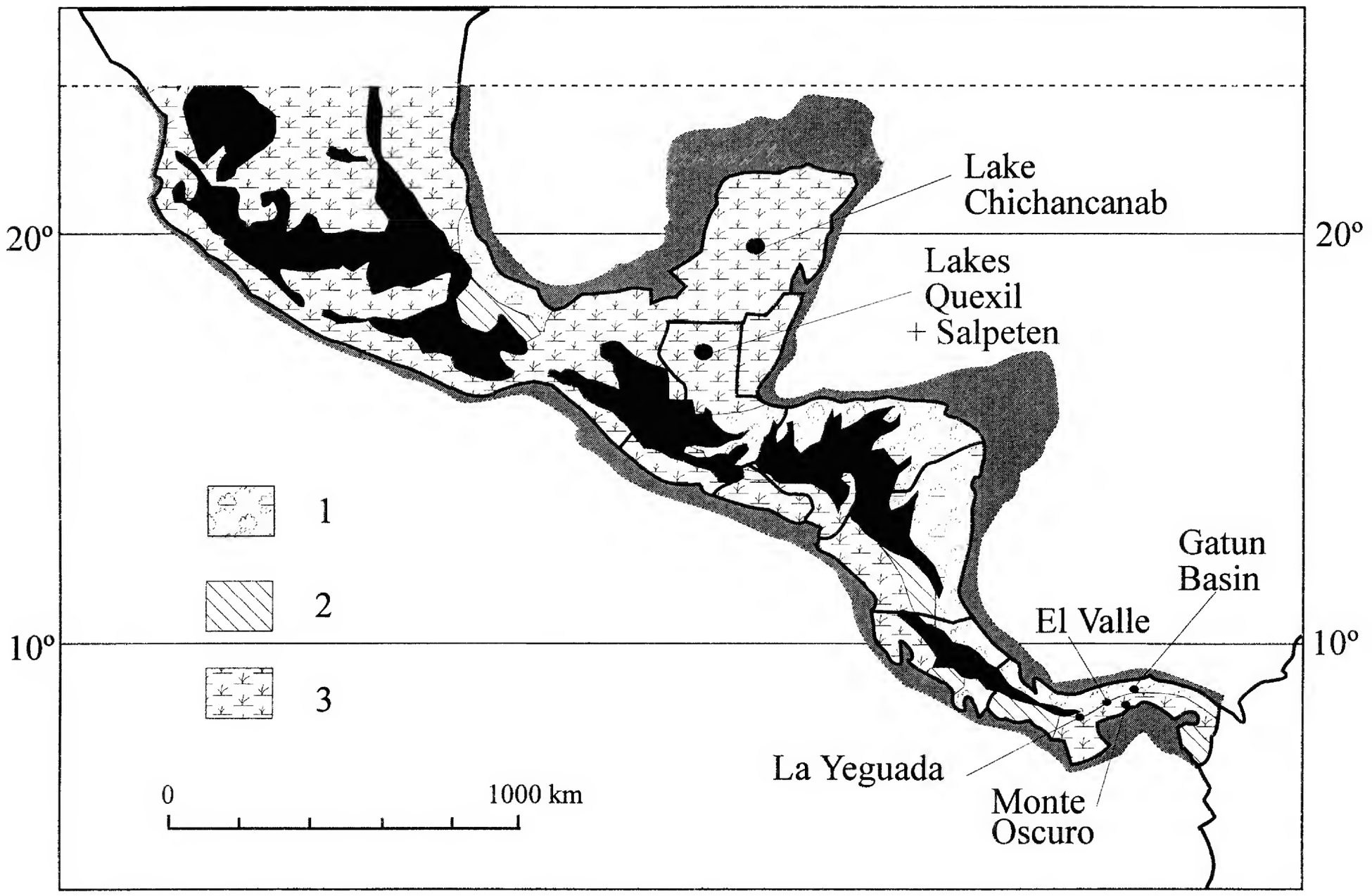


Figure 6.21. Diagram map of vegetation types in lowland tropical middle and Central America reconstructed for between 20,000 and ~10,500 years B.P. with location of paleoecological sites. 1 = Moist forest with mixture of current high-elevation (*Podocarpus*, *Alnus*, *Ilex*, *Quercus*) and lowland elements. Precipitation lower than at present but sufficient to support forest. 2 = Forest drier than today, patchy, with higher elevations containing more elements, and areas near the 2000 mm isohyet and areas with sandy soils supporting savanna woodland. 3 = Thorn woodland, low scrub, savanna with *Juniperus* (Guatemala), and gallery forest. Reprinted from Piperno and Pearsall (1998) and references cited therein, Academic Press, New York, with permission of Elsevier Science Publishers, Amsterdam.

[Northern Mexico—9000–4500 years B.P., Chihuahuan Desert moist; Sonoran Desert, warmer and drier]

(Central Mexico—moist)

~5780 ^{14}C years B.P.—forest decline, early human disturbance.

~3860 ^{14}C years B.P.—Twin Cays, Belize; mangrove; for ~240-year interval *Myrsine* (not currently present at the site) becomes dominant, suggesting hurricane disturbance or change in relative sea level (Wooller et al., 2004).

~2800 ^{14}C years B.P.—forest clearance, increased soil erosion, intense human disturbance; human disturbance in Cobweb Swamp 3400–500 years B.P., beginning of Maya clay deposition.

~1100–1000 ^{14}C years B.P.—forest recovery after decline of Classic Maya civilization (Haug et al., 2003); most Maya clay deposited <~1000 years B.P.

500 years B.P.—water level decreases at Cobweb Swamp due to reforestation after Maya collapse (Jacob & Hallmark, 1996).

There were similar moist intervals (or periods of increasing moisture) in an interstadial (~36–24 Kyr B.P.) of the Petén and from at least 34 to 23 Kyr B.P. in central Mexico; in the Late Glacial of the Petén (~12 Kyr B.P.) and the Chihuahuan Desert; and in the Petén (9000–6800 years B.P.), Chihuahuan Desert (9000–4500 years B.P.), and central Mexico. There were dry conditions in the Petén (~24–12 Kyr B.P.) and in central Mexico (to ~14 Kyr B.P.). This suggests the moist to wet-dry intervals were regional rather than local trends. In contrast, earliest Holocene times were relatively dry in the Petén, and wet and cool in the Sonoran Desert; while in the Petén it was moist to wet between 9000 and 6800 years B.P., dry in the Sonoran Desert, and at 6800 years B.P. moist in the Chihuahuan Desert. This suggests local differences and separate climate controls for the Atlantic and Pacific Ocean provinces of northern Mexico. These patterns can be considered further as additional

studies are completed on the Quaternary of northern Latin America.

The dynamic history and relatively recent age for the current version of the wettest plant formation in Guatemala is consistent with results for lowland wet forest associations elsewhere in Latin America and with results from study of the older middle Pliocene Paraje Solo flora of Veracruz, Mexico. Also evident are the same interacting forcing mechanisms for vegetation change in Guatemala as discussed for the Yucatán Peninsula—solar variations and Milankovitch cycles as they influence temperature, the amount and seasonal distribution of rainfall, and E/P ratios (e.g., Pleistocene aridity); sea-level changes as they affect water tables; vegetation changes (savanna to moist seasonal forest) with a feedback to climate via albedo and transpiration; and human impact. An approximation of the lowland vegetation of southern Mexico and Central America between ~20,000 and 10,000 years B.P. is shown in Fig. 6.21 (Piperno & Pearsall, 1998).

COSTA RICA

MIOCENE AND PLIOCENE (23.8–2.6 MA)

There is only a single plant megafossil flora published for Costa Rica, and that was more than 80 years ago. Berry (1921a) described 12 species among the genera *An(n)ona*, *Bü(y)ttneria*, *Ficus*, *Goeppertia*, *Heliconia*, *Hieronymia* (*Hieronyma*), *Inga*, *Nectandra*, *Piperites*, and *Phyllites costaricensis* (incertae sedis). They were collected by W. P. Woodring in 1917 from the "northeast border of Talamanca Valley on the west fork of Sheroli Creek [left scarp of the Sixaola Valley; 9.51°N, 82.61°W], about one-half mile above the forks, there being a waterfall and conglomerate precipice about 100 feet high at the latter locality." All the specimens (Table 6.1; Fig. 6.22) have entire margins, some have drip-tips, most are large (mesophyll leaf-size category; I: pp. 124–128), and they represent a wet phase of the lower to upper montane broad-leaved forest formation. The locality data are relatively specific, the site is accessible (Michael Grayum, pers. comm., 2006), and the collection was placed in the USNM, but no further studies have been made.

The geologic section at the locality is described as a basal sequence of marine fossiliferous beds called the Uscari shales (Cassell & Sen Gupta, 1989a, b; Bottazzi et al., 1994), overlain unconformably by a thinner series of sandstones and shales containing the plant megafossils. Berry (1921a, p. 169) believed the age of the fossils was "undoubtedly Miocene…younger rather than older Miocene." Recent work has shown the Uscari shale is Miocene, and that the overlying strata (Río Banano Formation) is Pliocene and probably middle Pliocene in age (Laurel Collins, pers. comm., 2002; Collins & Coates, 1999). The lower part of the Río Banano Formation in the Limón region is ~5.2–3.45 Ma in age (McNeill et al., 2000).

Individual plant megafossils have been described from other sites in Costa Rica, such as fern-like Pteridopsida (private collection, Río General Valley, 12 km southeast of San Isidro, San José Province, Térraba Formation, Oligocene to early Miocene; Gómez, 1970); *Karatophyllum bromelioides* (Bromeliaceae, San Ramón, Alajuela Province, Middle Tertiary; Gómez, 1972); *Palmacites berryanum* (Arecaceae, Pozo Azul, Puntarenas Province, Tertiary; Gómez, 1971); and Rhodophyta (red algae) possibly related to *Archaeolithothamnion*, *Goniolithon*, or *Lithothamnion* (Patarrá, San José Province, Tertiary; Gómez, 1973).

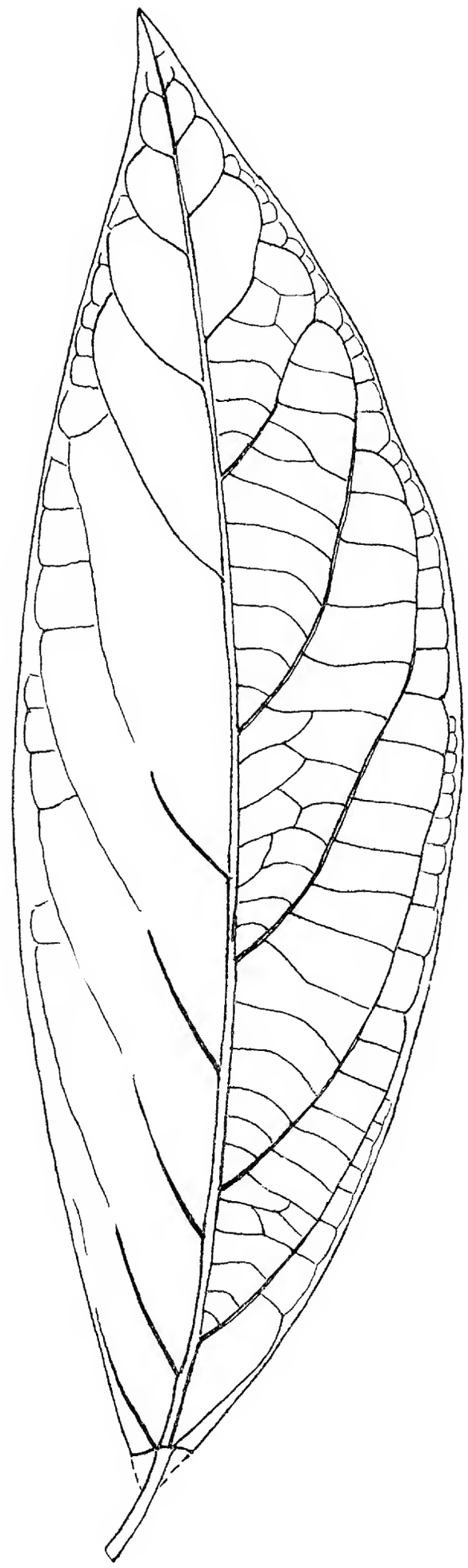


Figure 6.22. Sketch illustrating specimen of *Nectandra woodringi*, Río Banano Formation, Pliocene, Costa Rica. From Berry (1921a).

Two microfossil assemblages of Tertiary age have been published for Costa Rica. One came from the matrix of Berry's specimens previously described (Sheroli Creek, Río

Banano Formation, middle Pliocene; Graham, 1987a, c; Table 6.1). The identified taxa sort into three paleocommunities (some taxa range through several communities)—mangrove (*Rhizophora*); a lowland wet association of the lower to upper montane broad-leaved forest formation (*Phaeoceros*, *Cnemidaria*, Bombacaceae, *Alchornea*, cf. *Glycydendron*, cf. *Banisteriopsis*, cf. *Hiraea*, Myrtaceae [*Myrcia* type], and Melastomataceae); and a higher-altitude cloud forest association (estimated elevation 1000–1500 m; *Lycopodium*, *Selaginella*, cf. *Hymenophyllum*, *Lophosoria*, *Pityrogramma*, *Pteris*, *Podocarpus* [common], *Ilex*, Ericaceae [*Cavendishia* type], and *Lisianthius*). There is little or no evidence for plant formations of drier aspect, grasslands, or higher-altitude ceja or páramo, consistent with other Neogene floras of Central America.

The second plant microfossil flora is also from the Río Banano Formation but at Refinadora Costarricense de Petróleo's (RECOPE) experimental open pit mine near Zent in southeastern coastal Costa Rica (10°02'N, 83°17'W; Figs. 6.23–6.30; Graham & Dilcher, 1998). The locality is ~30 km south of Limón, and ~40 km to the north of Sheroli Creek. Pollen of the mangrove *Pelliceria* is present, rather than *Rhizophora* (Table 6.1), and it is a more lowland paleocommunity with *Lacmella* and *Symphonia* (both grow in the lowland wet forest), while the upland cloud forest genera of the Zent flora (e.g., *Podocarpus*) are absent. The two floras provide the only paleobotanical information available on the middle Pliocene vegetation and climates of coastal Costa Rica.

The present MAT in the region is ~26° C, MAP is ~3500 mm, and the paleoclimates were probably similar to slightly warmer and moister. The Río Banano Formation at the type section near La Bomba contains reef corals of which ~40% still grow in the region (Budd et al., 1999). A difference between the Río Banano flora of coastal southeastern Costa Rica and the Paraje Solo flora of coastal southeastern Mexico, both growing during about the same interval of middle Pliocene warmth, is that upwelling produced cooler conditions for the Paraje Solo flora and it grew adjacent to highlands of significant relief.

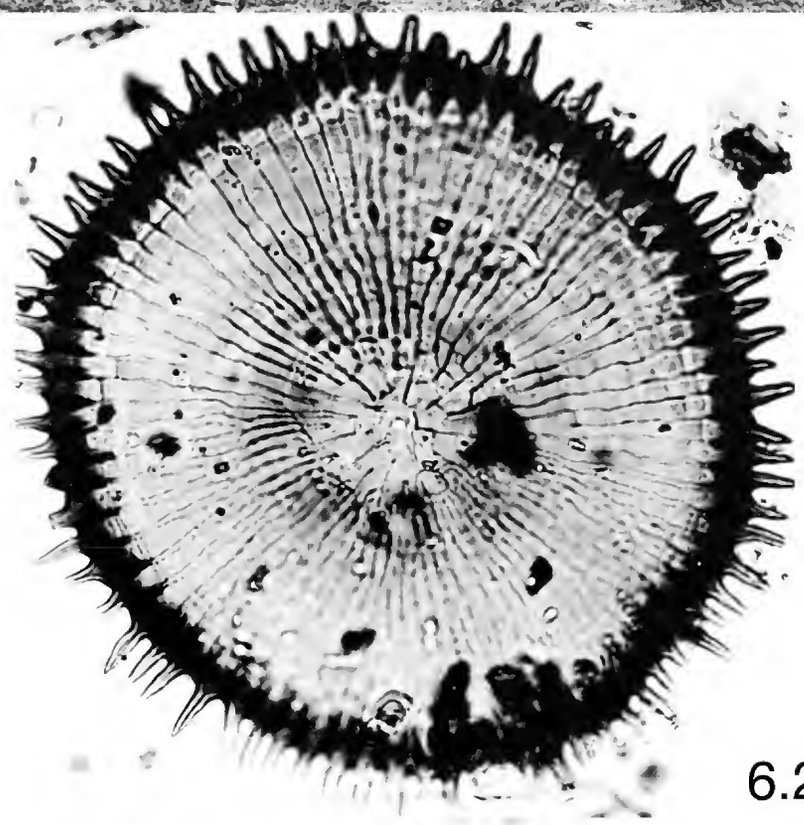
Modeling biomes and environments of the middle Pliocene warm period—Earlier in the text it was suggested that research in Neotropical biology is just entering the ecosystem phase, as defined here, for some intervals in a few regions. The middle Pliocene warm period (~3.29–2.97 Ma) and the cool trend that immediately followed is one such interval. The Paraje Solo, Sheroli Creek–Zent (Río Banano), and perhaps the Herrería floras are plant assemblages of northern Latin America deposited during the event. Modeling projects are under way that will provide a context for better interpreting these floras and the environments under which they grew. The U.S. Geological Survey's Pliocene Research Interpretation and Synoptic Mapping (PRISM) data set (Dowsett et al., 1994, 1999; http://pubs.usgs.gov/openfile/of99-535/) stores information on marine and terrestrial Pliocene environments. To approximate terrestrial Pliocene vegetation, PRISM2 uses 74 sites, mostly in northern North America and Europe, and assigns modern biome and environmental conditions to the Pliocene of other regions where there is insufficient data, which includes most of Latin America. Although new data continue to slowly accumulate, it will be a long time before adequate information exists for modeling middle Pliocene vegetation and climates in the Neotropics. In the meantime, Haywood et al. (2002) have made a first attempt at simulating global biomes and environments using a General Circulation Model (GCM; I: pp. vii–ix; United Kingdom Meteorological Offices' Unified Model or Hadley Centre Atmospheric Model Version 3) and the BIOME 4 vegetation model initialized with middle Pliocene boundary conditions. The BIOME 4 model predicts biome distributions under different climatic parameters. These models incorporate the terrestrial paleoclimate estimates derived from the paleofloras noted above.

Some preliminary results are of interest for Latin American vegetation. For the middle Pliocene, the model simulations predict a global MAT 2° C higher than at present, and a Northern Hemisphere tundra significantly reduced compared to its present extent. Translating this to northern Latin America, the areas suitable for cloud forest, ceja, and especially páramo adjusted upward or diminished to some extent. This further supports the suggestion made in Chapter 3 (Vegetation, Mexico) that, based on high levels of endemism, high diversity at the species rather than at the generic level, and orogenic histories, the current high-altitude vegetation of cold environments in Latin America is of relatively recent origin. The post-middle Pliocene would be a favorable time for their principal appearance as essentially modern plant formations.

During this interval in the Mediterranean region, cool conifer forests extended upward in distribution. In northern Latin America, the bosque de oyamel (with *Picea*), high-altitude pine forests, and to the south shrubby páramo, occupied comparable sites. Following the middle Pliocene period of warmth, other upland vegetation zones (e.g., cloud forest) were probably lowered and brought closer to lowland basins of deposition. The simulations also imply overall higher sea levels than at present with greater inundation of lowlands, consistent with the documented elevated levels at several localities (e.g., Fig. 6.16), so that the extent of habitats available to the lowland Neotropical rain forest and coastal swamps would have been less. Desert vegetation is less extensive in the lower latitudes in the middle Pliocene simulations due to an increase in rainfall of ~6%, and it is replaced by shrubland/chaparral–woodland–savanna. This identifies the post-middle Pliocene as a favorable time for intensifying the trend toward true desert vegetation in North America (southwestern U.S. and northern Mexico) that began at the end of the early Miocene and that would be completed during the dry intervals of the Quaternary. All the predictions are preliminary, especially for the lower latitudes where data are scarce. Nonetheless, the methodology shows promise for analyzing extensive amounts of complex information and, with continuing refinement, it offers predictive value for past vegetation–environment interactions.

6.23

6.24



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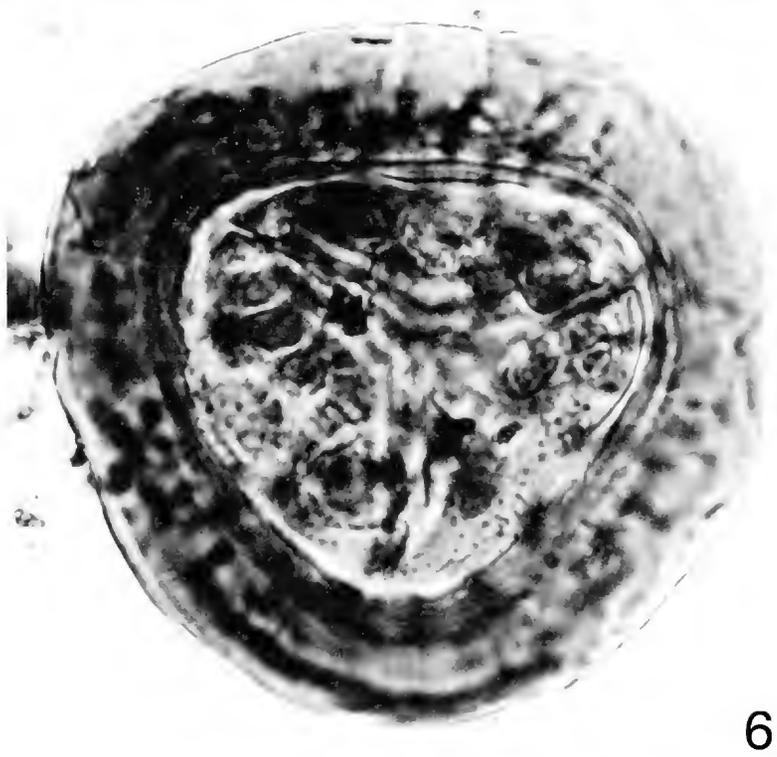

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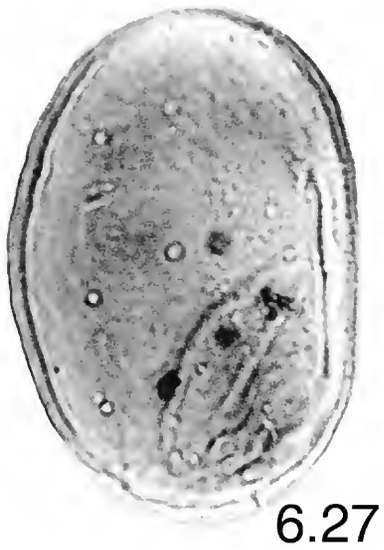

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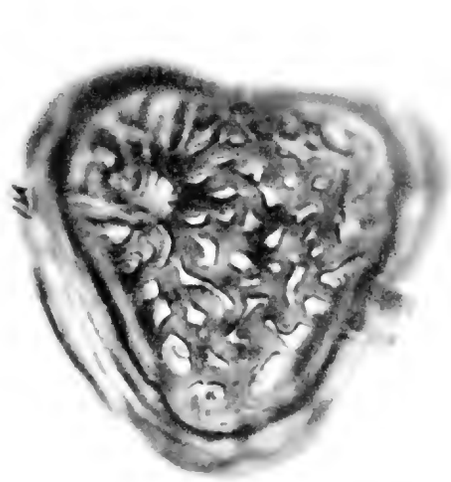

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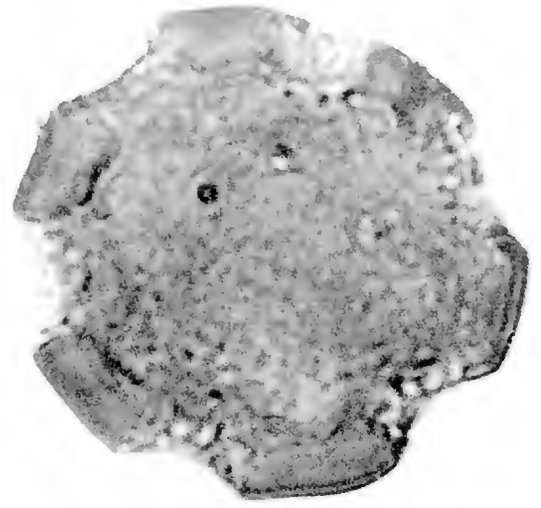


6.30

Figure 6.23. Collection locality at RECOPE experimental open pit near Zent, Costa Rica.

Figure 6.24. Close-up of collecting horizon in the Pliocene Río Banano Formation, Zent, Costa Rica.

Figures 6.25–6.30. Microfossils from the Pliocene Río Banano Formation, Zent, Costa Rica. 6.25. *Microthyrium*-type ascomycete reproductive structure. 6.26. *Lophosoria*. 6.27. Monolete fern spore (*Laevigatosporites*). 6.28. Monolete fern spore (*Verrucatosporites*). 6.29. *Pityrogramma*. 6.30. *Symphonia*.

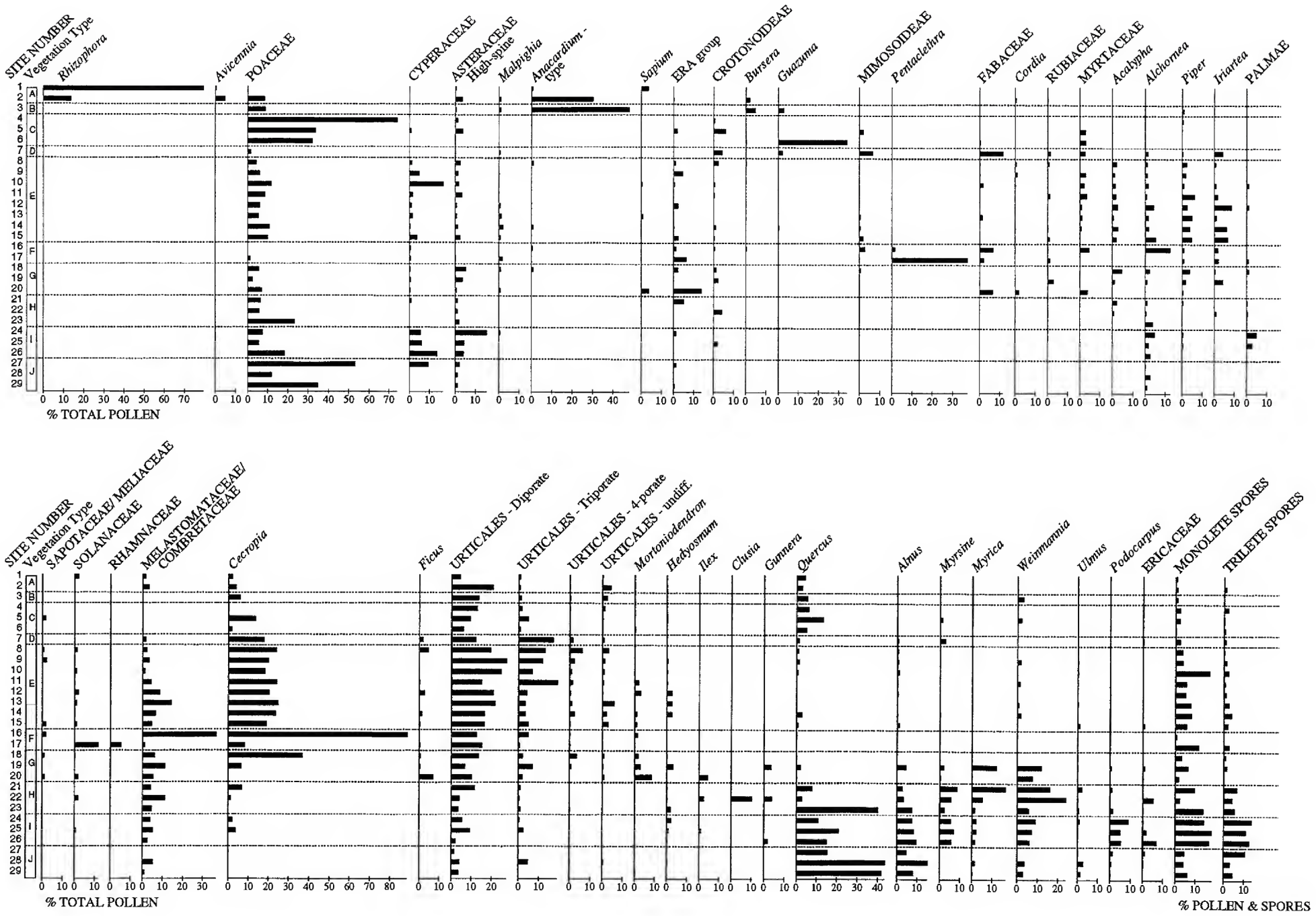


Figure 6.31. Diagram of modern pollen rain percentages for various vegetation types in Costa Rica. Reprinted from Rodgers and Horn (1996), with permission of Elsevier Science Publishers, Amsterdam.

QUATERNARY (2.6 MA–PRESENT)

A modern pollen rain study was made for 10 vegetation types in Costa Rica—mangrove, tropical dry forest, derived savanna, tropical moist forest, tropical wet forest, lowland freshwater swamp, premontane rain forest, montane rain forest, montane bog, and páramo (Rodgers & Horn, 1996; Fig. 6.31). One result was that no one pollen type dominated the pollen rain of all communities. Recall that in the mountainous regions of central Mexico, pollen of *Pinus*, and to some extent *Quercus* and *Alnus*, was prominent in all communities and, thus, over-represented throughout the pollen diagrams. In the Costa Rican samples, the pollen spectra generally reflected the vegetation in the immediate vicinity (e.g., *Rhizophora* in mangrove swamp, Poaceae in derived savanna and páramo). There were exceptions, however, such as large amounts of *Cecropia* pollen found in the modern lowland freshwater swamps. Such studies are useful reminders of the generalized nature of paleocommunity and paleoenvironmental reconstructions based on palynological evidence, and the value of ancillary information from independent sources.

An example is the combined contribution from palynology (Horn & League, 2005) and geomorphology in estimating MATs in the highlands of Costa Rica (Orvis & Horn, 2000). Quaternary moraines at ~3500 m on Cerro Chirripó in the Cordillera de Talamanca show four glacial advances, and the ELA reflect an average temperature lowering of 7°–8° C below the present 7.2° C, or near ~0° C. The present lapse rate is 5.4° C/km, calculated as follows: ~7° C at the summit, 26° C in the lowlands, for a 19° C difference ÷ 3.5 km = 5.4° C/km lapse rate. This yields a MAT in the lowlands at the glacial maxima of ~19° C, or ~7° C lower than at present. This is lower than at some other sites such as Lake La Yeguada, Panama (5° C lower between ~19,100 and ~13,000 years B.P.; Bush et al., 1992), and El Valle, Panama (5°–6° C between 16,800 and 11,400 years B.P.; Bush & Colinvaux, 1990), and about the same as at Lake Quexil, Guatemala (6.5°–8° C between ~24,000 and ~14,000 years B.P.; Leyden et al., 1993). However, Lake Quexil is ~8° latitude farther north (~17° vs. ~9°N); it is closer in time to the Last Glacial Maximum compared to Chirripó I in Costa Rica (after 12,330 years B.P. and before 9700 years B.P., end of Younger Dryas chronozone; deglaciation date of ~10,000 ^{14}C years B.P. [Horn, 1990]), and it is situated in a somewhat less maritime environment than the more coastal site in Costa Rica. Taking these differences into account, an

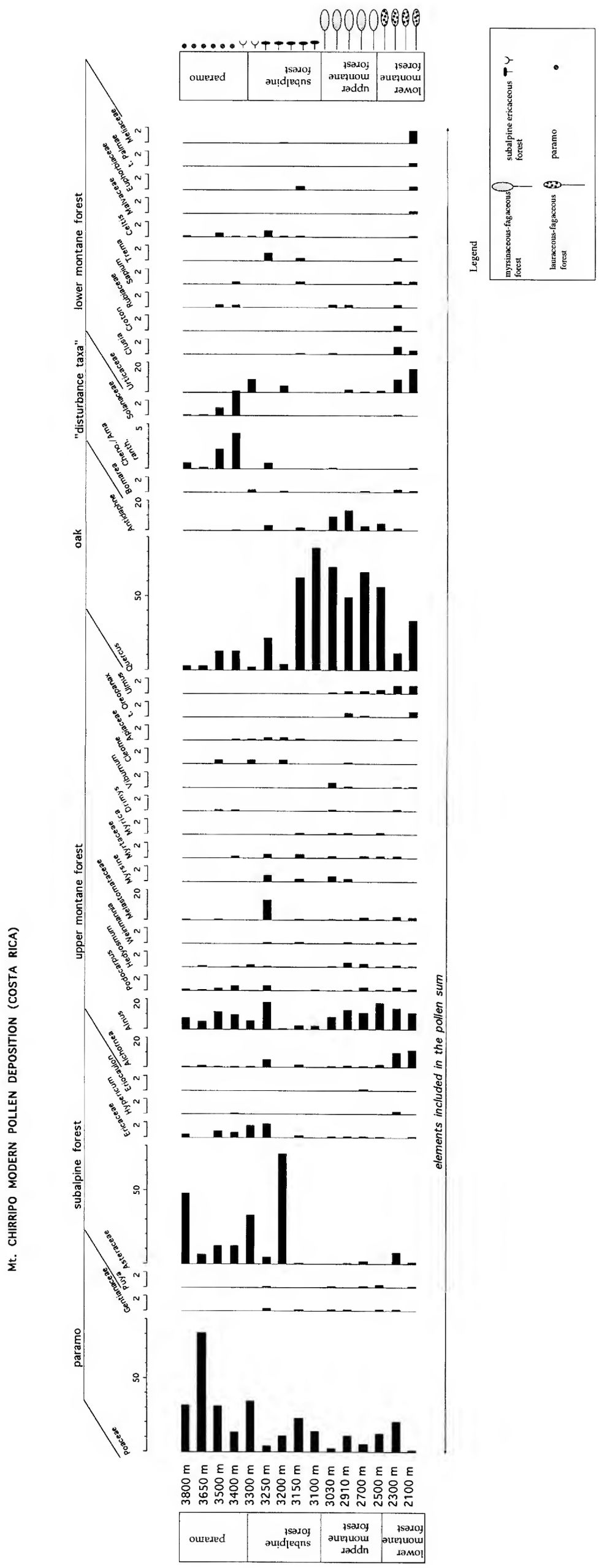


Figure 6.32. Diagram of modern pollen rain percentages along an altitudinal gradient (2100–3800 m) on Cerro Chirripó, Costa Rica. Reprinted from Islebe and Hooghiemstra (1997), with permission of Elsevier Science Publishers, Amsterdam.

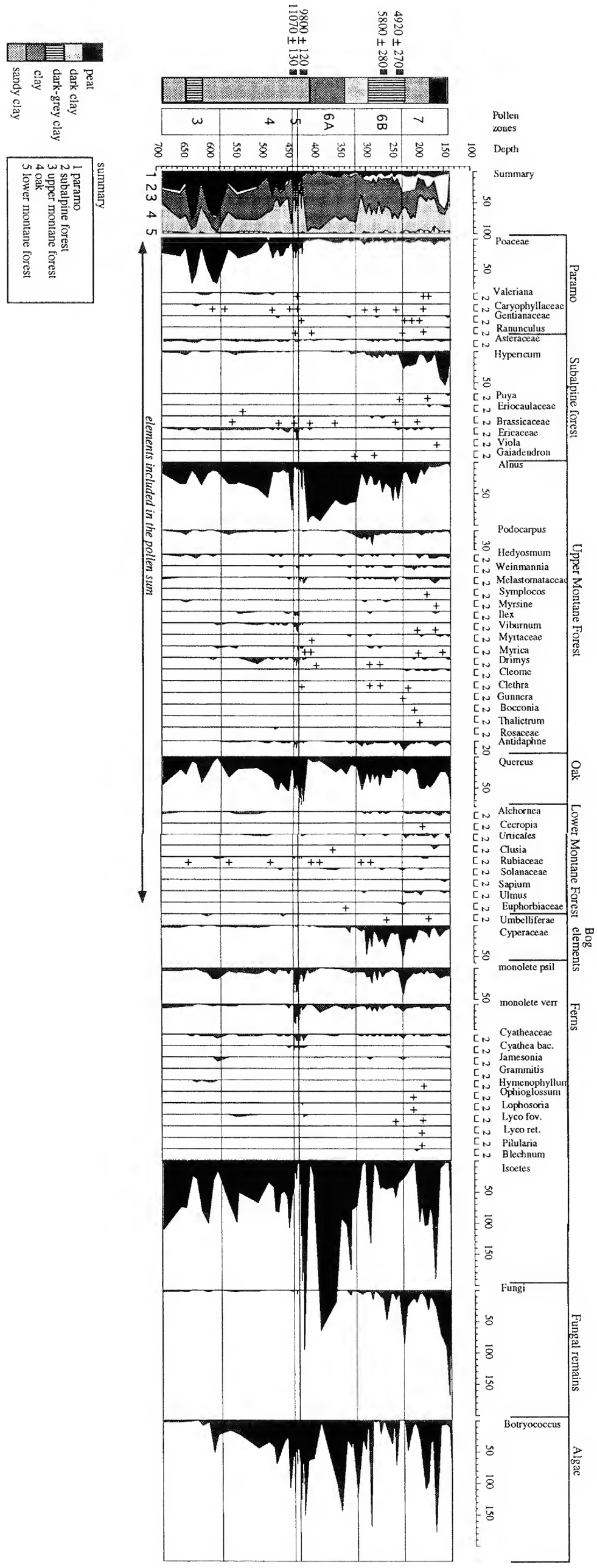


Figure 6.33. Spore and pollen diagram of La Chonta-I (2310 m) section, Cordillera de Talamanca, Costa Rica. Reprinted from Islebe and Hooghiemstra (1997), with permission of Elsevier Science Publishers, Amsterdam.

approximation of MAT trends in the lowlands at the LGM (~24,000 years B.P.) is as follows: ~6°–7° C below the present at the Guatemala site, ~5°–6° C at the Costa Rica and Panama sites, and ~4°–6° C in the Amazon lowlands (e.g., 5° C for the Brazilian lowlands; Stute et al., 1995). For comparison, MAT is estimated 7°–9° C cooler in the Colombian highlands and somewhat less in the southern Central Andes Mountains (see later section). It is worth recalling that if these temperature values, and all the fluctuations known to have occurred within them, are demonstrated for the last glacial–interglacial cycle, roughly similar values can be assumed for each of the 18–20 previous cycles within the past ~2.6 Ma.

Early palynological studies of late Quaternary sediments from Lachner Bog, Cordillera de Talamanca, Costa Rica (9°43'N, 83°56'W; Martin, 1960, 1961), suggested that cold intervals affected the páramo, as shown by zones where *Lycopodium* and especially *Isoetes* spores were abundant and *Quercus* and other montane forest tree pollen were scarce. This was interpreted to reflect cold conditions at ~20,750 years B.P. when páramo extended an estimated 600 to 800 m below its present limit.

Another early study (Kesel, 1983) integrated Quaternary geomorphic features in the Río General Valley of southwestern Costa Rica with an examination of palynomorphs from surface and outcrops samples. Pliocene marine sediments are overlain by Pliocene volcanics indicating that major uplift occurred in about the middle Pliocene. During the Quaternary, erosion of the uplifted strata produced alluvial fans, and contributed sediments to form the Brujo Formation in the valley. Lakes developed in the valley and those lacustrine sediments provided the material earlier examined by Martin (1960, 1961). Analysis of the Brujo samples by Kesel (1983) showed high percentages of grasses, and *Acacia*, *Acalypha*, and *Byrsonima*, reflecting savanna-like vegetation and dry conditions in the late Pleistocene. Recall this was the time of Pleistocene aridity and savanna and juniper shrub in the Petén of Guatemala (Leyden, 1984).

There are other studies on the Quaternary vegetation and environments of Costa Rica by Driese et al. (2007), Hooghiemstra et al. (1992), Islebe and Hooghiemstra (1995, 1997), Islebe (1996), Islebe et al. (1995, 1996a, b), and Kappelle (1996). The latter cores are from bogs at La Chonta (2310 m altitude; 9°41'N, 83°57'W) and La Trinidad (2700 m; 9°50'N, 84°W) in the Cordillera de Talamanca and extend back an estimated 80,000 years B.P. The studies also include modern pollen rain data along an altitudinal transect from 2100–3800 m on Mt. Chirripó (Fig. 6.32). The modern forest belts are the páramo (3800–3300 m), subalpine forest (3500–3000 m), upper montane forest (3300–2400 m), and lower montane forest (2400–1500 m; Kapelle et al., 1989, 1995). In the oldest part of the profile (Fig. 6.33) extending into the Early Glacial there were fluctuations at 2300–2800 m that shifted the surrounding forest between subalpine rain forest and upper montane rain forest. At maximum glaciation (50,000–13,000 years B.P.) the forest line fell to ~2000 m altitude and páramo grew around the La Chonta site. In the more warm and moist Late Glacial (~14,000 years B.P.), tree line extended up to 2700–2800 m altitude, and the vegetation was an upper montane oak forest. This was the time that the range of temperate oaks was expanding in the lowlands of Guatemala (Leyden et al., 1994), and similar humid conditions prevailed in the highlands of Mexico (Lozano-Garcia & Ortega-Guerrero, 1994). Oak pollen reached 80% in some parts of the profile, and modern pollen rain studies from the Guatemalan highlands revealed that only ~5% is attributable to long-distance transport (Islebe & Hooghiemstra, 1995). Then temperatures fell by an estimated 1.5°–2.5° C for ~580 years, dropping tree line to 2400 m during a time corresponding to the Younger Dryas event. The vegetation was *Alnus* shrub. In the Holocene, tree line extended up to 3300–3500 m and the landscape above was covered by a subpáramo of Asteraceae, Ericaceae, *Escallonia*, and *Puya* as at present. The maximum change in tree line during the time represented by the La Chonta sediments was ~1400 m, based on a estimated lapse rate of 5.7° C/km, representing a temperature depression at 2300 m of ~7°–8° C in the highlands of Costa Rica at the LGM (Hooghiemstra et al., 1992; Islebe & Hooghiemstra, 1997).

Human occupation and land disturbance in Costa Rica—The oldest human artifacts from Costa Rica are Clovis and Magellean spear points like those used 12,000–10,000 years B.P. (Snarskis, 1981). Records older than the Late Glacial stage (~14,000–10,000 years B.P.) need confirmation (Cooke, 1998). The evidence for land disturbance and cultivation is as follows:

- 2000 years B.P.—Laguna Santa Elena (8°56'N, 82°56'W, 1100 m elevation), pollen of *Zea mays*, disturbance taxa, charcoal, continuous human occupation for last 2000 years (Anchukaitis & Horn, 2005).
- 2560 years B.P.—Laguna Bonilla (9°59'39"N, 83°36'11"W), Laguna Bonillita (9°59'36"N, 83°36'47"W), lower eastern slope of Volcán Turialba, *Zea mays* pollen, charcoal, clearance of *Myrsine* (drop in pollen percentage) at ~1300 years B.P. (Northrop & Horn, 1996).
- 2700 years B.P.—La Selva (10°26'N, 83°59'W), *Zea mays* pollen (Kennedy & Horn, 1997; Horn & Kennedy, 2001).
- 3000 years B.P.—Laguna Zoncho (8.813°N, 82.963°W), *Zea mays* pollen, charcoal (Clement & Horn, 2001).

PANAMA

LATE EOCENE (41.3–33.7 MA)

The fossil record for the Cenozoic of the canal region is relatively extensive, and central Panama is one of the paleontological hotspots in Central America. There are no Paleocene or early Eocene floras for Panama, or indeed for all of northern Latin America, but independent lines of evidence indicate this was a time of considerable global warmth (I: pp. 88, 162–175).

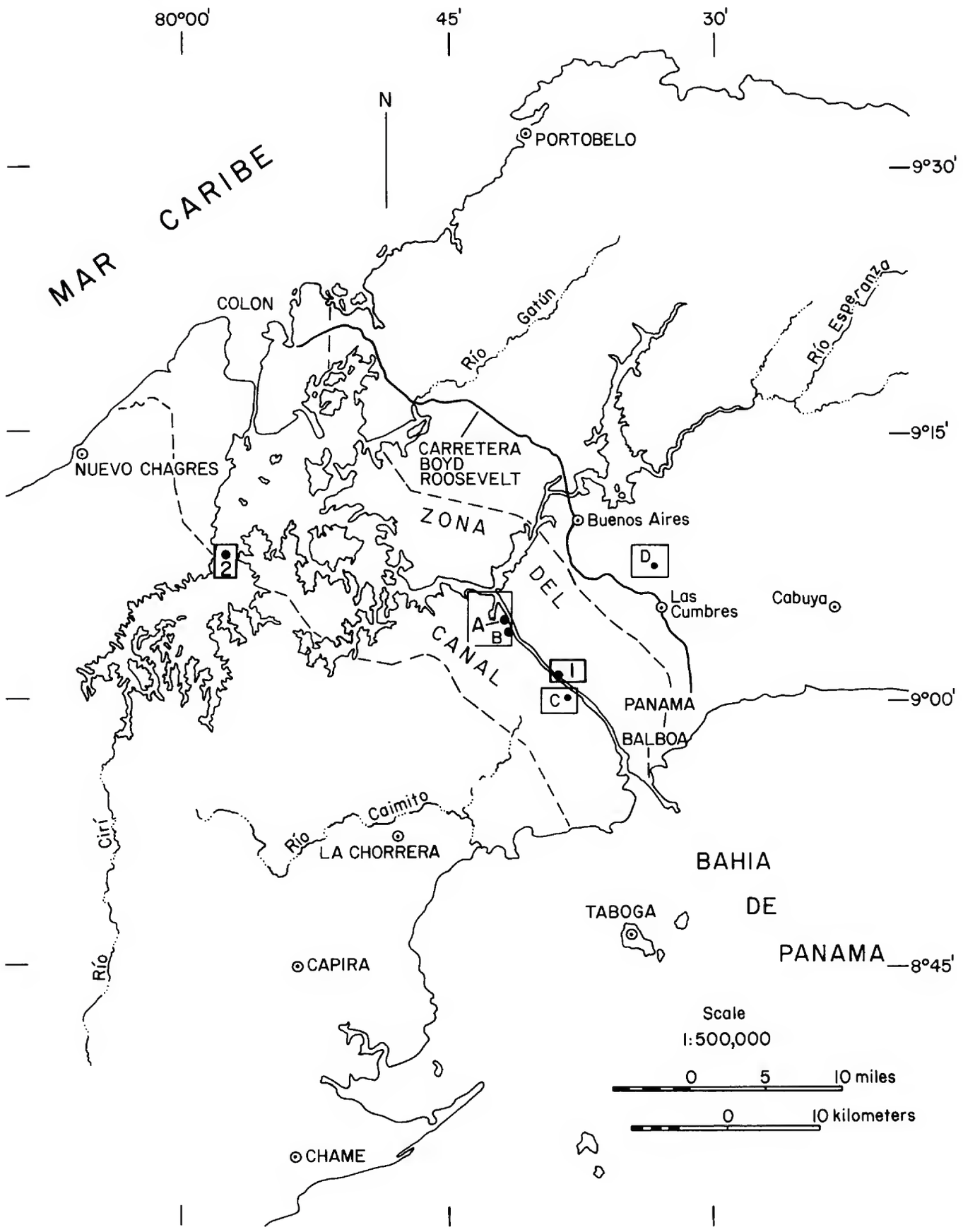


Figure 6.34. Map of Tertiary spore and pollen-bearing localities, Panama. A, B = La Boca Formation, Las Cascadas Reach of Gaillard Cut, Panama Canal. C = Cucaracha Formation, Culebra–Cucaracha Reach. D = Gatuncillo Formation, near Alcalde Díaz (Peñocito). 1 = Drilling site through the Culebra Formation, Contractor's Hill locality. 2 = Drilling site through the Gatún Formation, Gatún Lake.

Sea surface temperatures were higher than at present in the lower latitudes by 4°–5° C during the LPTM, likely due in part to greater atmospheric CO_2 concentration (Zachos et al., 2003), and conditions were at least as warm as at present in the middle and late Eocene (see below).

The oldest known microfossil assemblage for Panama is from the Eocene Gatuncillo Formation (Graham, 1985; Graham et al., 1985) outcropping along a road cut just off the Boyd-Roosevelt highway (9°7'N, 79°32'W; D in Fig. 6.34). The deposit is a fault-bounded fragment of land that emerged when the western margin of the Caribbean Plate was being defined, and when the Greater Antilles volcanic arc was colliding with the Bahamas Platform. The formation consists of mudstones, siltstones, quartz sandstone, impure bentonite, coralline and foraminiferal limestone, and lenses of lignite from a few centimeters to 1–2 m in thickness. The depositional environment was coastal because the lignites contain *Pelliceria* and *Rhizophora*, and the corals indicate tropical conditions. The mollusks are species typical of the middle to late Eocene (Woodring, 1957–1982), and among the larger foraminifera, 18 of the 21 species are characteristic of the late Eocene, three are found in the middle Eocene, and two of these (*Yaberinella jamaicensis* and *Fabiania cubensis*) are middle Eocene species (Cole, 1952). The age of the spore and pollen-bearing lignites is probably late Eocene.

A total of 87 spore and pollen types were recognized from the Gatuncillo Formation, and 48 have been identified, representing about half of the palynomorphs encountered in the assemblage (Table 6.1; Figs. 6.35–6.39). Among the most abundant (3% or more) were *Selaginella* (Fig. 6.35), *Ceratopteris* (= *Anemia* fide Dettmann & Clifford, 1992), trilete fern spores (types 1–5), monolete fern spores (types 1–5), Arecaceae (types 1–5), cf. Araliaceae, *Coccoloba*, *Combretum–Terminalia* (Graham, 1980), *Crudia*, *Faramea* (Fig. 6.36), cf. *Ficus* (Fig. 6.39), *Lisian-*

thius (Fig. 6.37; Graham, 1984), *Pelliceria* (Graham, 1977), and *Rhizophora* (Graham, 1995). New records of *Sphaeropteris–Trichipteris* and *Mortoniodendron* (Fig. 6.38; Graham, 1979), *Eugenia–Myrcia* (Graham, 1980), *Sabicea* (Graham, 1987b), and others (Graham, 1990) are included in the updated lists in Table 6.1.

Given the age of the flora (late Eocene, ~41.3–33.7 Ma), the restricted and disrupted extent of the landscape, and low to moderate physiographic relief, the taxa do not sort readily into paleocommunities based on modern analogs. There are 40 designated unknowns in the Gatuncillo flora compared to 14, 2, 15, and 27 for the Miocene Culebra, Cucaracha, La Boca, and Gatún floras, respectively (Table 6.1), and several taxa range through more than one community. An approximation of the plant formations present in the Eocene of Panama is as follows:

Shrubland/chaparral–woodland–savanna (9 taxa; limited, individual elements probably restricted to edaphically controlled, local habitats; tropical dry forest–premontane dry forest in the Holdridge system): *Cardiospermum*, *Casearia*, *Coccoloba*, *Combretum*, *Eugenia*, cf. *Ficus* (Fig. 6.39; see also Horn & Ramirez B., 1990), *Serjania*, *Tetragastris*, cf. *Tillandsia*.

Mangrove (2 taxa): *Pelliceria*, *Rhizophora* (comparatively rare, maximum 10%).

Beach/strand/dune (4 taxa): Arecaceae, *Casearia*, *Coccoloba*, *Terminalia*.

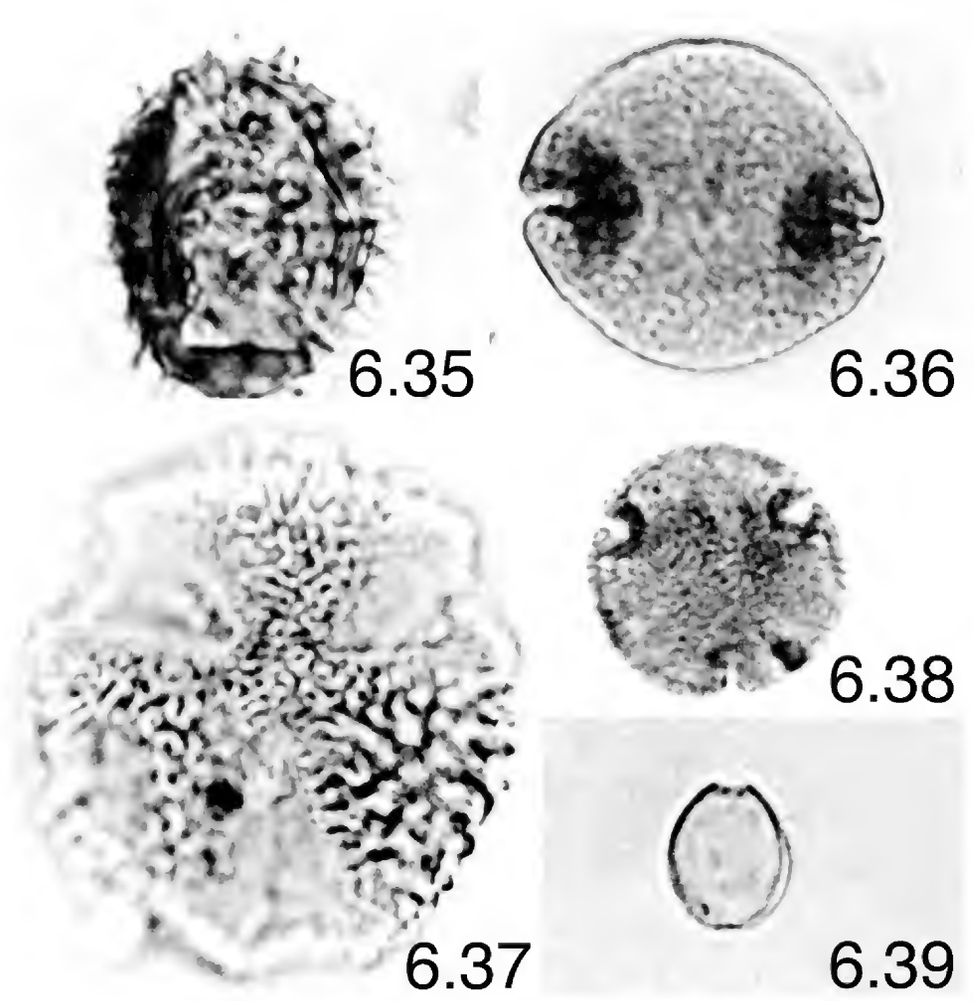
Aquatic (1 taxon): *Ceratopteris* (or *Anemia*, open well-drained habitats, mostly up to 1000 m in Central America [Tryon & Tryon, 1982]).

Lowland Neotropical rain forest (17 taxa; low wet phase of the lower to upper montane broad-leaved forest; tropical wet forest, tropical moist forest, premontane rain forest, premontane wet forest, premontane moist forest in the Holdridge system): *Selaginella*, *Pteris*, *Campnosperma*, *Chrysophyllum*, *Combretum*, *Crudia*, *Faramea*, *Ficus*, *Mortoniodendron*, *Myrcia*, *Paragonia*, *Paullinia*, *Protium*, *Terminalia*, *Tetragastris*, *Tillandsia*, *Tontelea*.

Lower to upper montane broad-leaved forest (9 taxa): *Anemia*, *Pteris*, *Alfaroa–Oreomunnea*, *Casearia*, *Ilex* (drier habitats), *Lisianthius*, *Paullinia*, *Serjania*, *Tillandsia*.

There is no evidence for desert, grassland, coniferous forest, tundra, or páramo. Pollen of the Cyperaceae, Poaceae, *Typha*, or other types common in freshwater herbaceous bog/marsh/swamp formations was not recovered, and the habitats were likely local and ephemeral.

Paleoenvironmental conditions are difficult to estimate from the limited paleobotanical evidence. Many of the genera in the Gatuncillo flora presently grow along the moist northern (Atlantic) side of Panama, as opposed to the drier Pacific side, consistent with the absence of highlands that presently deflect moist winds coming from the east. On Barro Colorado Island, the current annual temperature range on the forest floor is between 32° and 21° C, and the MAT is 28° C. The annual precipitation on Barro Colorado Island ranges from 2717 to 3251 mm (107–128 inches). MAP at Colón (Atlantic side) is 2717 mm (107.3 inches), compared to 1727 mm (68 inches) at Balboa on the Pacific side. The warm wet climates of present-day northern coastal Panama approximate conditions in the Eocene, consistent with the widespread tropical vegetation during that epoch.

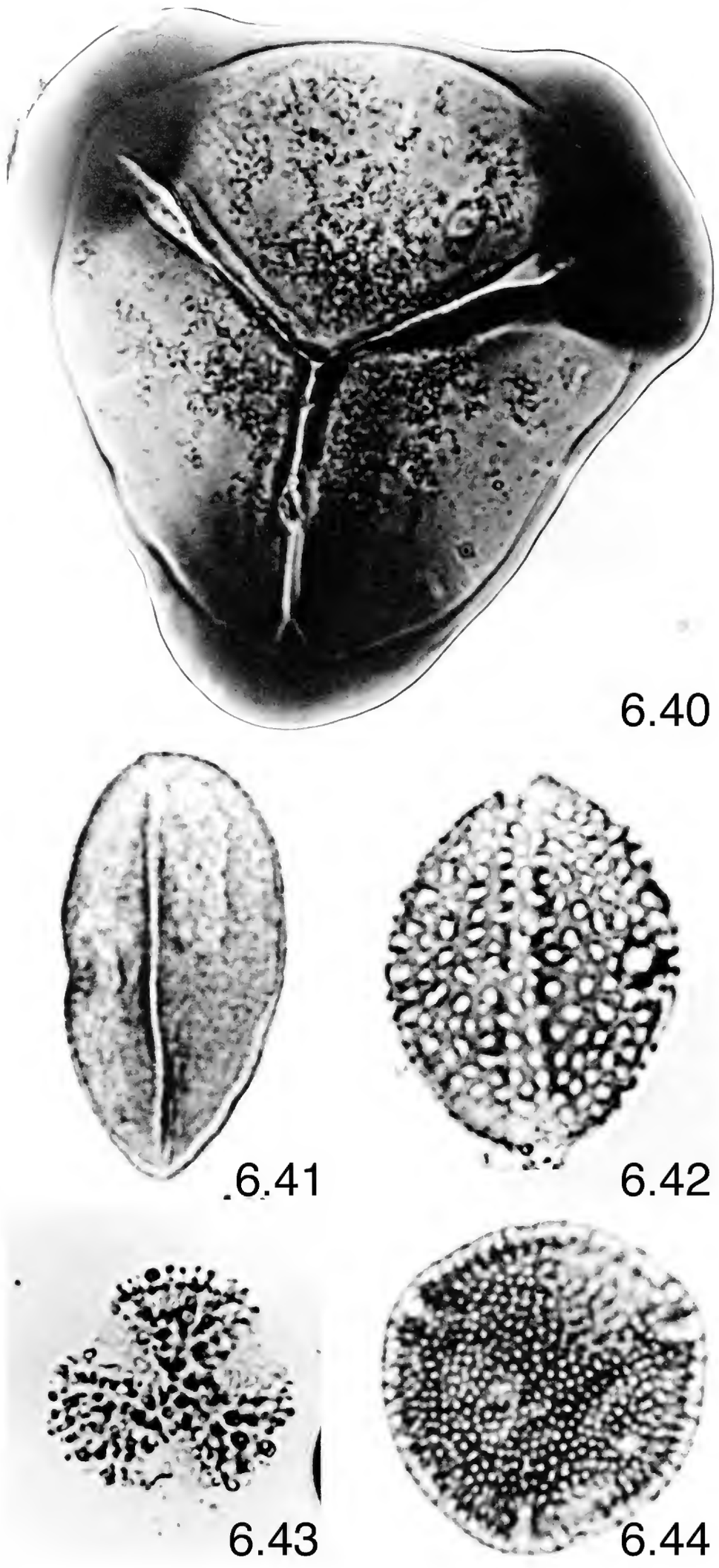


Figures 6.35–6.39. Microfossils from the late Eocene Gatuncillo Formation, Panama. 6.35. *Selaginella*. 6.36. *Faramea* (diporate form). 6.37. *Lisianthius*. 6.38. *Mortoniodendron*. 6.39. cf. *Ficus*.

MIOCENE (23.8–5.3 MA)

Megafossil plants from Panama were mentioned by Berry (1914), a palm nut was described from the Gatún Formation of the former Canal Zone (*Iriartites vaughani*; Berry, 1921b), and a palm fruit was described from the province of Chiriquí in western Panama (*Palmocarpon geonomoides*; Berry, 1928), all Miocene in age. The most extensive list of megafossil plants (listed as Neogene in Table 6.1) was reported by Berry (1918) from scattered localities within the former Canal Zone. They came from the Bohío, Culebra, Cucaracha, Caimito, and Gatún formations. Most came from the Culebra Formation exposed along the Gaillard Cut, and from one-fourth mile south of Empire Bridge. With the exception of one plant considered to be an Eocene (?) species (*Diospyros macdonaldi*), the rest were thought to be of Sannoisian (earliest Oligocene) to Burdigalian (early Miocene) age. In addition to questions of identification, the provenance is too imprecise for community or environmental reconstructions or to be of value in tracing lineages. The specimens are in the USNM, should the assemblage or a particular lineage be of interest.

Several plant microfossil floras of Miocene age are known from the canal region of Panama. These include the early Miocene Culebra (Figs. 6.40–6.44), Cucaracha (Figs. 6.45–6.46), and La Boca floras (Figs. 6.47–6.48; Graham, 1988a, b, 1989),



Figures 6.40–6.44. Microfossils from the early Miocene Culebra Formation, Panama. 6.40. *Lygodium*. 6.41. Palmae, *Manicaria* type. 6.42. Palmae, *Cryosophila* type. 6.43. *Ilex*. 6.44. *Sabicea*.

and the late middle to late Miocene Gatún flora (Table 6.3; Collins & Coates, 1999; Graham, 1991a, b, c). The three early Miocene floras were deposited at the continent-ocean interface as evident from microfossils of *Acrostichum* type, *Hibiscus* type, and *Rhizophora*. Some chenoam and Asteraceae pollen are present, consistent with the mostly early Neogene appearance and later diversification of these types in other regions. Compared to the plant formations of the Eocene, those of the early Miocene are more diverse, better defined based on comparison with the modern analogs, and include more specimens that can be referred to extant taxa. Tracing the modernization of Central American terrestrial plant communities is hindered, however, by the lack of transitional floras of Oligocene age in the region. Global MAT and MAP were trending toward colder, drier, and more seasonal climates, but the local low-lying physiography, low latitude (9°N), and insular setting partially offset these trends. A MAT of ~28° C and a MAP of ~107 inches, toward the lower range for the late Eocene, would account for the similarity between the Miocene communities and the modern vegetation of northern coastal Panama. The following is an estimate of the early Miocene plant formations of central Panama, based on the Culebra, Cucaracha, and La Boca floras:

Shrubland/chaparral–woodland–savanna (11 taxa; limited, individual elements probably restricted to edaphically controlled, local habitats; tropical dry forest–premontane dry forest in the Holdridge system): *Lygodium*, *Acacia*, *Allophylus*, *Casearia*, chenoams, cf. *Combretum* (as *Combretum–Terminalia*), Asteraceae, cf. *Eugenia* (as *Eugenia–Myrcia*), cf. *Guazuma*, *Matayba*, cf. *Rourea*.

Mangrove (4 taxa): cf. *Acrostichum*, cf. *Hibiscus* (as *Hampea–Hibiscus*), *Pelliceria*, *Rhizophora* (abundant, maximum 88%).

Beach/strand/dune (4 taxa): Poaceae, Arecaceae, *Casearia*, cf. *Terminalia* (as *Combretum–Terminalia*).

Aquatic (2 taxa): *Ceratopteris*, *Utricularia*.

Lowland Neotropical rain forest (30 taxa; low wet phase of the lower to upper montane broad-leaved forest; tropical wet forest, tropical moist forest, premontane rain forest, premontane wet forest, premontane moist forest in the Holdridge system): *Lycopodium*, *Selaginella*, cf. *Antrophyum*, *Cyathea*, *Dannea*, *Lygodium*, *Pteris*, *Cryosophila* type, *Desmoncus* type, *Manicaria* type, *Synechanthus* type, *Alchornea*, *Allophylus*, *Casearia*, *Combretum* (as *Combretum–Terminalia*), *Crudia*, *Cupania*, *Dioscorea* (as *Dioscorea–Rajania*), cf. *Doliocarpus*, cf. *Eugenia* (as *Eugenia–Myrcia*), *Guazuma*, cf. *Hampea* (as *Hampea–Hibiscus*), *Ilex*, *Matayba*, cf. *Pouteria*, cf. *Rourea*, *Sabicea*, *Sapium*, cf. *Terminalia* (as *Combretum–Terminalia*), *Tetrorchidium*.

Lower to upper montane broad-leaved forest (7 taxa): *Lycopodium*, *Selaginella*, *Cyathea*, *Pteris*, *Alfaroa–Oreomunnea* (first appearance in Panama), *Manicaria* type, *Sapium*.

The late Miocene Gatún flora was obtained from cores drilled by the Panama Canal Company in 1962 from Gatún Lake. Up to eight core segments ~2 m long, stored in boxes (Fig. 6.46) stacked 8 feet high, filled a facility the size of an airplane hangar. The amount of geophysical, geochemical, paleomagnetic, paleontological, and other kinds of information on the Neogene and Quaternary of central Panama was incalculable. The collection was discarded into Gatún Lake because of space limitations, but samples had been taken for various studies, including ones for the dissertation of Alexan-

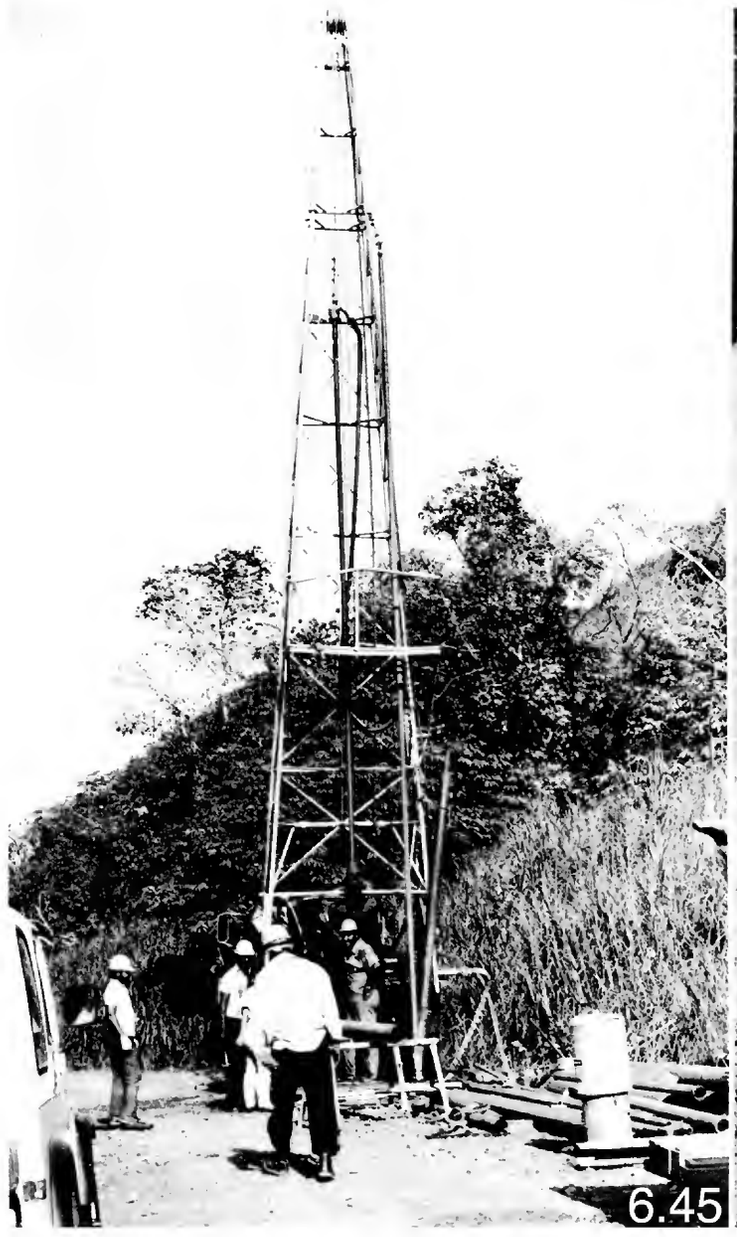


Figure 6.45. Drilling operation with portable drill from truck bed, Cucaracha Formation, canal region, Panama.

Figure 6.46. Core from the Cucaracha Formation and small core box.

dra Bartlett (Bartlett & Barghoorn, 1973) on the Quaternary palynology of Panama. These included some sediments from the underlying Miocene Gatún Formation, and subsequently others were obtained from the Tertiary part of the cores and from field collections. The Gatún Formation had been assigned to the middle Miocene (Cooke et al., 1943; Woodring, 1957–1982; Stewart & Stewart, 1980), and later marine gastropod faunas suggested an age of Pliocene (Vokes, 1983; Willem van den Bold, Robert Stewart, pers. comm., 1990; Graham, 1991a, b, c). The recent consensus is that it is 11.8 to 8.6 Ma (late middle Miocene to late Miocene; Collins & Coates, 1999). The microfossils are from the upper part of the section and are regarded here as late Miocene in age. The composition of the Gatún flora is shown in Table 6.1, and the taxa sort into the following paleocommunities (alternative similar pollen for some genera as above):

Shrubland/chaparral–woodland–savanna (12 taxa; tropical dry forest, premontane dry forest): Poaceae, *Acacia*, *Allophylus*, *Bursera*, *Cedrela*, *Ceiba*, cf. *Combretum*, cf. *Eugenia*, cf. *Jatropha*, *Posqueria*, *Pseudobombax*, *Serjania*.

Mangrove (2 taxa): cf. *Hibiscus*, *Rhizophora*.

Beach/strand/dune (2 taxa): Poaceae, *Bucida*.

Freshwater herbaceous bog/marsh/swamp (including fringing shrubby/woody vegetation) (>3 taxa): monolete fern spores (several types likely representing Blechnaceae, Polypodiaceae, Pteridaceae), Arecaceae, *Bucida*.

Aquatic (3 taxa): *Ceratopteris*, *Cabomba*, *Utricularia*.

Lowland Neotropical rain forest (37 taxa; low wet phase of the lower to upper broad-leaved montane forest; tropical wet forest; premontane wet forest): *Lycopodium*, *Selaginella*, *Alsophila*, *Cnemidaria*, *Ctenitis*, *Cyathea*, *Ophioglossum*, *Pteris*, *Aegiphila*, cf. *Aguiaria*, *Alchornea*, *Allophylus*, *Bernoullia*, *Bucida*, *Bursera*, *Cedrela*, *Chomelia*, cf. *Cionosicys*, *Combretum–Terminalia*, *Cosmibuena*, *Crudia*, *Cupania*, *Cymbopetalum*, *Erythrina*, *Eugenia–Myrcia*, *Faramea*, *Guarea*, *Hampea*, cf. *Jatropha*, *Mortoniodendron*, *Paullinia*, *Petrea*, *Posoqueria*, *Pseudobombax*, *Serjania*, cf. *Stillingia*, *Symplocos*.

Lower to upper montane broad-leaved forest (34 taxa; mostly lower wet phase; premontane moist forest, premontane rain forest, lower montane moist forest, lower montane wet forest, montane moist forest, montane wet forest): *Lycopodium*, *Selaginella*, *Ophioglossum*, *Alsophila*, *Cyathea*, *Grammitis*, *Pteris*, *Podocarpus*, *Acacia*, *Alfaroa–Oreomunnea*, *Aegiphila*, *Alchornea*, *Allophylus*, *Bernoullia*, *Bursera*, *Ceiba*, cf. *Cionosicys*, *Combretum–Terminalia*, *Cosmibuena*, *Cymbopetalum*, *Eugenia*, *Erythrina*, *Faramea*, *Hampea*, *Hauya*, *Ilex*, *Paullinia*, *Petrea*, *Posoqueria*, *Pseudobombax*, *Quercus*, *Serjania*, cf. *Stillingia*, *Symplocos*.

There is no evidence for desert, grassland, coniferous forest, páramo (including ceja), or tundra vegetation.

One of the interesting aspects of studying the historical component of ecosystem evolution is to observe the changes that become evident as an increasing number of floras are available for study. This is especially true when these changes correlate with alterations in climate and physiography from independent lines of evidence. Such opportunities are rare in

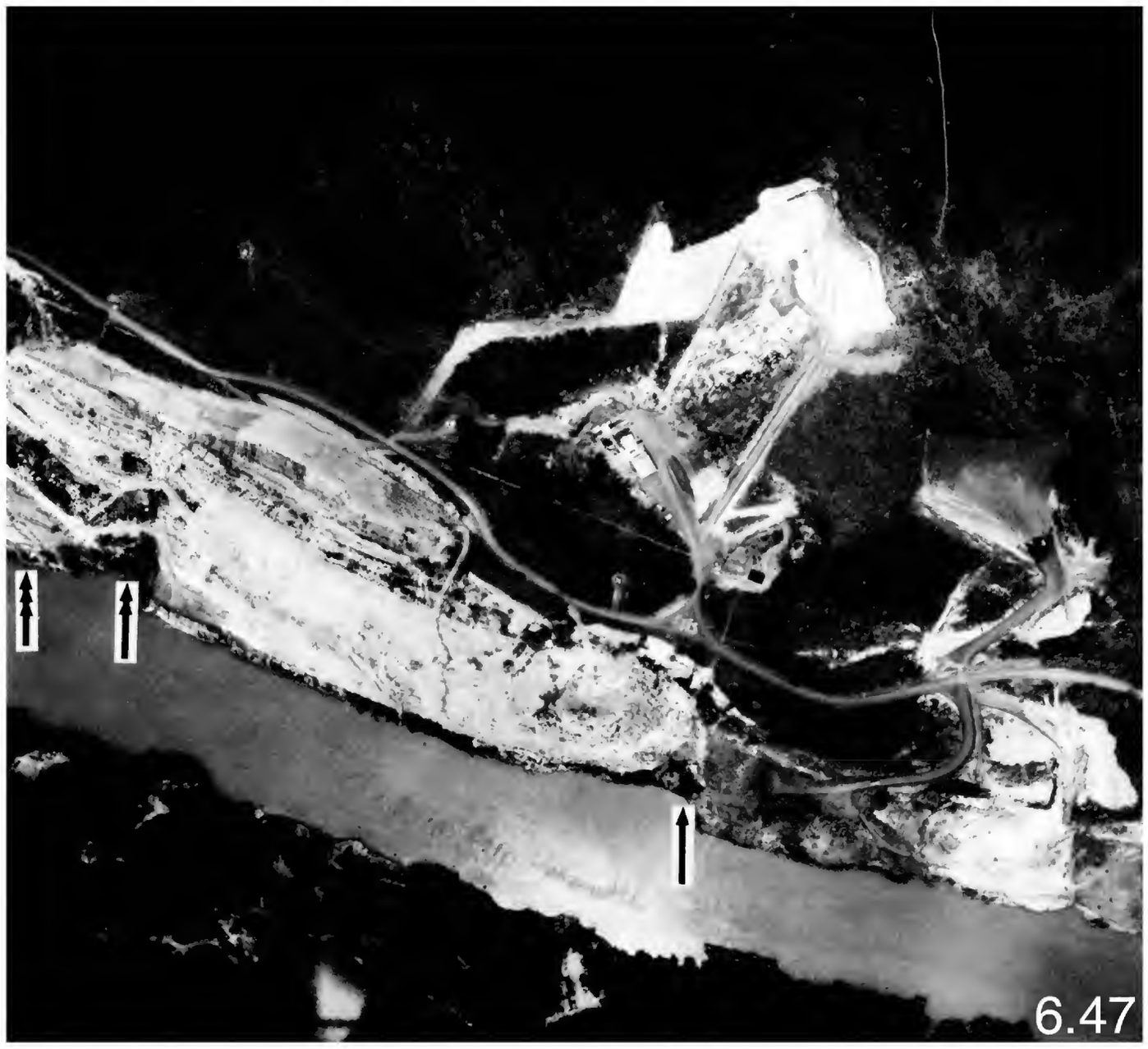


Figure 6.47. Aerial photograph of Las Cascadas Reach, Panama Canal, taken in 1967 when this section of the canal was being widened from 90 m to 155 m. Arrows designate collecting localities in the La Boca Formation. Maintenance and construction along the canal have removed or repositioned many of the outcrops sampled in earlier studies. Photograph provided by Robert Stewart, Panama Canal Co.

Figure 6.48. Exposure of the La Boca Formation along the Panama Canal corresponding to single arrow in Fig. 6.47. Note the fault terminating the white tuff at the lower left of the exposure (see Fig. 2.29).

the tropics, but one is provided by the Panama assemblages. The late Miocene Gatún flora differs from the preceding early Miocene assemblages in several ways (Table 6.3). There is a slight increase in overall diversity (86 to 109 taxa), community types (6 to 7), and in the number of component species in each community. The most noticeable trend, however, is in the lower to upper montane broad-leaved forest (9 to 34 taxa) and the increasing representation of temperate forest elements. This, in turn, is a reflection of a more complex landscape resulting from continued volcanism, compression between the Caribbean, North American, and South American plates and subplates, and subduction along the Middle American Trench (Chapter 2, Figs. 2.19, 2.27, 2.30, 2.31).

Another stage in the modernization of the vegetation in

Table 6.3. Trends in the modernization of central Panamanian vegetation based on the late Eocene Gatuncillo; early Miocene Culebra, Cucaracha, and La Boca (C/C/L); and late Miocene Gatún floras. S/C–W–S = shrubland/chaparral–woodland–savanna; B/S/D = beach/strand/dune; FWH/B/M/S = freshwater herbaceous/bog/marsh/swamp (including associated woody species); LNRF = lowland Neotropical rain forest; LUMBF = lower to upper montane broad-leaved forest.

	Gatuncillo	C/C/L	Gatún
Total number of taxa (diversity)	86	92	109
Plant formation/number of component taxa:			
S/C–W–S	9	11	12
Mangrove	2	4	2
B/S/D	4	4	4
FWH/B/M/S	0	0	3
Aquatic	1	2	3
LNRF	17	30	37
LUMBF	8	7	34
Temperate forest elements			
Podocarpus	0	0	1
Alfaroa–Oreomunnea	0	1	1
Quercus	0	0	1

the isthmian region is shown in the better representation of dry elements and drier plant formations. For example, in the Gatún flora, there are 12 taxa that potentially represent the shrubland/chaparral–woodland–savanna formation (including a rise in Poaceae pollen to 7.5%), compared to a maximum of four (plus two widespread) in the late Eocene Gatuncillo flora, seven in the early Miocene Culebra flora, and none in the early Miocene Cucaracha and La Boca floras. The same physical change that made for increasing habitat and terrestrial plant diversity (the presence of greater highlands) also began deflecting moisture-laden winds from off the Atlantic Ocean by the late Miocene, initiating a drier Pacific side.

If more complex landscapes were providing a greater variety of habitats, and highlands were beginning to create drier conditions along the southern side of Panama, then an increase in temperate elements would be expected. In Panama, *Podocarpus*, *Alfaroa–Oreomunnea*, and *Quercus* first appear in the Gatún flora, reflecting the evolution of the landscape, and the global temperature trend toward cooler temperatures, less precipitation, and greater seasonality. The barrier previously mentioned through the Darién–Atrato region still existed and was a factor in keeping *Alnus* from entering South America until ~1 Ma ago, and *Quercus* until ~330,000 years ago.

QUATERNARY (~2.6 MA TO PRESENT)

The first detailed study of Quaternary vegetation history in Panama was by Bartlett and Barghoorn (1973) from seven cores drilled by the Panama Canal Company in Gatún Lake. One sample was dated at 35,500 ± 2500 years B.P., and others at ~12,000 years B.P. to the present. In contrast to the upland sites of the Cordillera de Talamanca in Costa Rica and the High Plain of Bogotá in Colombia, the Gatún sediments record the complex interactions between sea level, climate, and landscape in a coastal environment. In addition to the complicated physical setting, many global climate changes (Younger Dryas, Heinrich, D–O events) and their manifestation in tropical latitudes were not well known, and there was the unrecognized source of error from fluctuating amounts of radiocarbon in the atmosphere. Phillips et al. (1997) question the association of *Myrica–Ilex* with cooling and increased seasonality, and the proposed interstadial low-stand in sea level at 35,000 years B.P. needs confirmation (Bush et al., 1992). Other results have proved more consistent with later studies, including the considerable change the vegetation has undergone even at this low latitude (~9°N) and in a coastal and insular setting. There were relative changes in sea level as reflected by the presence, absence, and abundances of *Rhizophora* and other mangrove communities; a temperature lower than at present by an estimated 2.5° C at ~12,000 years B.P. (Younger Dryas = ~12,800–11,500 years B.P.) and presumably even lower at the LGM; and a dry interval in the mid-Holocene (~7300–4200 years B.P.).

In a more recent study, a 55-m core was obtained from lacustrine sediments of an extinct caldera lake at 500 m above sea level near El Valle to the east of Gatún Lake (Bush & Colinvaux, 1990; Fig. 6.49). The upper 15 m cover the time from >30,000 years to the present. Prior to 14,000 years B.P. oaks extended ~1000 m below their present lower elevations, and later in the Late Glacial (14,000–10,000 years B.P.) they were ~700 m lower for an estimated (at least seasonal) temperature depression of 4°–6° C. It was drier than at present between 30,000 and 12,000 years B.P. (driest during pollen zone EV4[3]). It has been suggested that the highlands were a refuge for rain forest taxa during dry intervals (Whitmore & Prance, 1987), but Bush and Colinvaux (1990) believe this is unlikely. Whether it was dry enough in the lowlands for grassland–(oak) savanna vegetation to isolate versions of the rain forest into refugia-like parcels is a subtle distinction to make from pollen admixtures given the approximate nature of the technique (Fig. 6.49; Chapter 8). However, even at the time of maximum cooling and lower elevations of *Quercus* populations, pollen of warm lowland tropical taxa persisted.

Gentry (1985) suggests that *Quercus* and other taxa in the modern highlands of western Chiriquí and in the eastern Darién (Cerro Tacarcuna, 1900 m) indicate migration through the intervening central tropical lowlands. As mentioned previously, the paleobotanical evidence shows some tropical vegetation in the lowlands throughout the interval, and the oaks present in these disjunct montane regions consist of 11 species of *Quercus* in Chiriquí and a single endemic species in Darién. Whether some populations of *Quercus* extended into intervening local habitats at the time of maximum coolness and dryness (e.g., on Cerro Jefe) is also too subtle to determine with certainty from pollen assemblages. Nonetheless, a lowering of *Quercus* below its present altitudinal limits during cool-dry intervals, possibly with scattered intervening populations, affords an explanation

that involves (shorter) long-distance dispersal and (more) continuous populations. This scenario is probably better in accord with the complexity of the system and the limitations of the method than interpretations suggesting direct migration across the lowlands.

A pollen sequence from Lake La Yeguada (elevation 650 m; 8°27'N, 80°51'W; 14.3 Kyr B.P. to the present) also shows that in the cool and dry Late Glacial, montane *Quercus* and *Magnolia* (phytoliths), with *Gunnera*, *Ilex*, and *Symplocos*, grew an estimated 900 m below their present elevation for a temperature lower by ~5° C than at present (Bush et al., 1992). Climates between 14.3 and 13.5 Kyr (Late Glacial–interglacial transition) fluctuated considerably, consistent with the profiles from Lake Valencia, Venezuela (Leyden, 1985). Holocene climates were generally warmer and more moist than in the Late Glacial, although there was a dry phase between 8200 and 5500 years B.P., when lake levels were lower. Humans were present in Panama between 11 and 10 Kyr B.P. (projectile points and other artifacts; Bird & Cooke, 1978; 12–10 Ma in Costa Rica), and human disturbance of the vegetation is evident after 11 Kyr B.P. from land clearing, increased organic carbon, cultivars, charred phytoliths, and starch grains of maize and manioc on grinding stones dated 7000–6000 years B.P. (Piperno et al., 2000; Piperno, 2006). At Lake La Yeguada, *Zea* phytoliths are found at 4000 years B.P., and *Zea* pollen just above sediments dated to 5860 years B.P. (Piperno et al., 1990, 1991a, b; Piperno & Pearsall, 1998, p. 225). *Zea* pollen and phytoliths are recorded at 7000 ^{14}C years B.P. at the nearby Cueva de los Ladrones rock shelter (Piperno et al., 1985).

Climatic trends may be compared for Guatemala, Costa Rica, and Panama for the Late Glacial and Holocene as interpreted from palynological information. Similarities likely reflect regional climate-forcing mechanisms, while differences could be due to local conditions, insufficient evidence, or the need to reassess some data sets. The patterns for Guatemala and Costa Rica are comparable, while the interpretation of some records for Panama are different. According to the summary by Islebe and Hooghiemstra (1997, p. 599):

> "Piperno et al. (1991a) and Bush et al. (1992) indicate for Lake La Yeguada (650 m elevation, Panama) during the period from 16,000 to 11,000 B.P. [Late Glacial] a temperature decrease of ca. 5°C compared with modern conditions, suggesting that this period was cooler than the period from 20,000 to 18,000 B.P. This is unlike northern Central America and the palynological data from the Talamancan mountains. We expect the Late glacial in Costa Rica to be 3–4°C colder than at present.
>
> Relatively dry conditions prevailed during this period in both regions until 11,000 B.P. A sudden cooling of 1.5–2.5°C in the Cordillera de Talamanca is indicated between 11,000 and 10,400 B.P. (Islebe et al., 1995), which is also recorded in Lake Quexil (Leyden et al., 1994, lowland Guatemala). This episode seems to fall into a period of a southward shift of the northernmost position of the ITCZ. The record from Lake La Yeguada (Bush et al., 1992, Panama) does not show cooling following the interpretation of the authors. Leyden (1995) suggests that monsoonal conditions may have blocked cooler conditions. Bush et al. (1992) assumed the period 11,000–10,500 B.P. in Panama to be a transitional one to warmer and wetter conditions. Leyden (1995) suggests a transition in the watershed vegetation rather than warming at Lake La Yeguada, as some of the lowland taxa are also indicative of disturbance. Bartlett and Barghoorn (1973) suggested that between 11,300 and 9600 B.P. temperatures were 2.5°C lower than present day for the Panamanian Canal Zone, which coincides more with the Costa Rican and Guatemalan case.
>
> At the onset of the Holocene an increase in precipitation is registered around 10,400–9800 B.P. in Costa Rica and Guatemala. Palaeoecological studies by Leyden (1984, 1987; Leyden et al., 1994) and Islebe et al. (1996b) from different Guatemalan lowland lakes showed a drier rapid development to moist early Holocene lowland forests. These moraceous (*Brosimum*) dominated forests seem to be established around 8600 B.P. based on new wood radiocarbon dates from Lake Petén Itzá devoid of hard water errors (Islebe et al., 1996b). Montane forests seem to develop in the Cordillera de Talamanca in the same period (Islebe et al., 1996a). In Panama establishment of lowland evergreen forest at La Yeguada is also indicated at ca. 8600 BP (Piperno et al., 1991a)."

A summary of precipitation trends through Central America is provided by Piperno and Pearsall (1998, p. 96):

> "Estimates of the amounts of precipitation reduction have ranged from 25% to 50%. Leyden (1984), considering the nature of the vegetation change recorded in Venezuela and Guatemala, believes that reduction may have been on the order of approximately 50%. We believe that, on the basis of the presence of late-glacial thorn woodland and savannas on the Panamanian Pacific Coastal Plain, precipitation was reduced by at least 35% in lower Central America, whereas van der Hammen and Absy (1994) use an estimate of between 25% and 40% for Amazonia. . . .
>
> Colinvaux (1993) believes that precipitation reduction was more modest, being on the order of no more than 10%–20%. However, his estimate is based on data derived from the CLIMAP modeling of sea surface temperatures that have been shown to be too low by at least 50%, and the data fail to account for the drastic vegetational changes observed in many lowland areas. A reduction of sea surface temperature on the order of 5° C, which now appears likely,

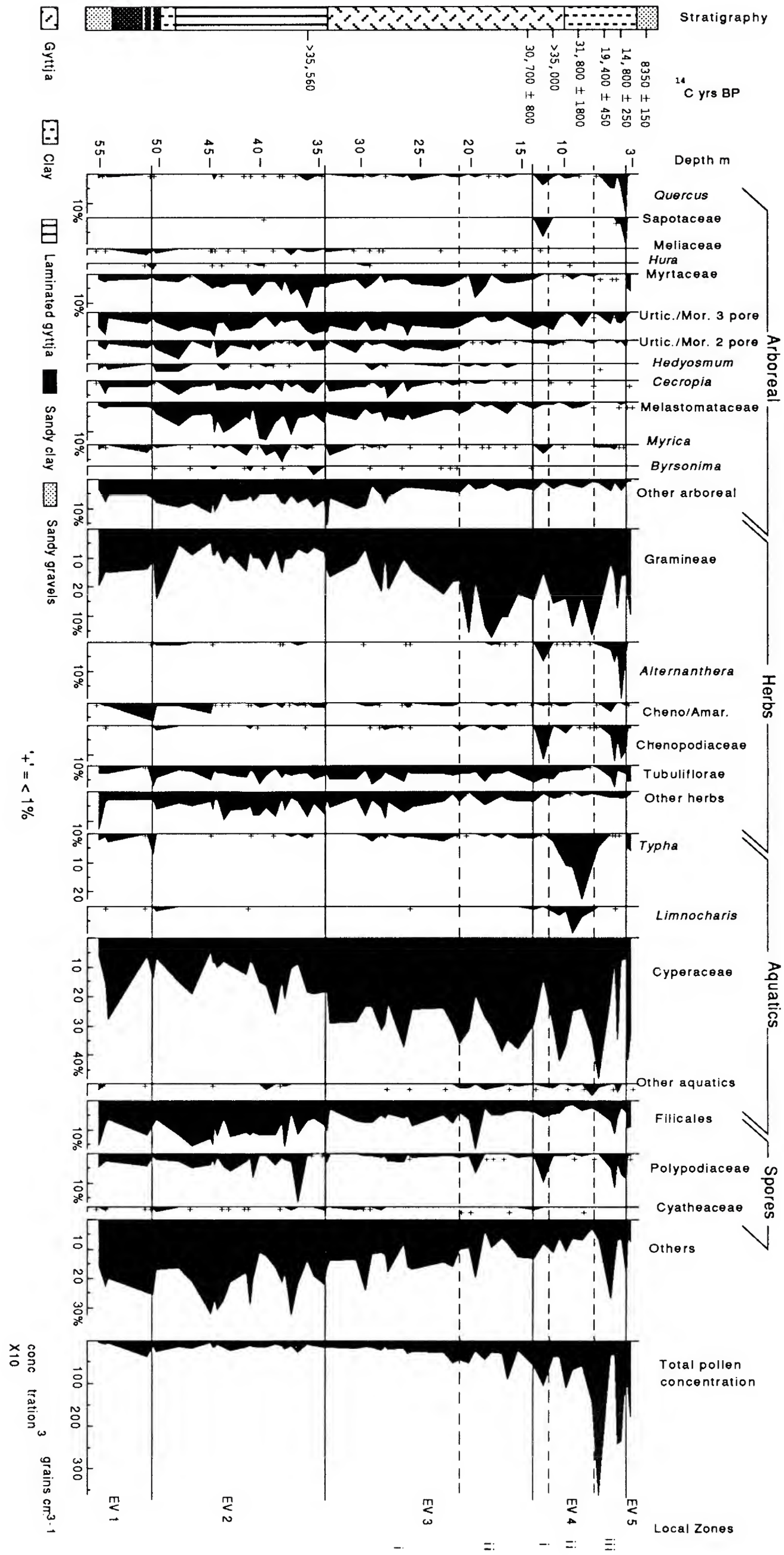


Figure 6.49. Spore and pollen diagram from El Valle, Panama. From Bush and Colinvaux (1990). Used with permission of Opulus Press, Uppsala, Sweden.

Table 6.4. Age of Cretaceous and Tertiary formations/floras of northern Latin America cited in the text and in Tables 4.1, 5.1, and 6.1 according to the original authors and recent age estimates. DSDP = Deep Sea Drilling Project.

Formation/flora	Time	Estimated age (Ma)
Mexico		
La Misión	Campanian	83.5–71.3
Rosario	Campanian	83.5–71.3
Tarahumara (Huepac Chert)	Maastrichtian	71.3–65
Olmos	Maastrichtian	71.3–65
Piedras Negras	Maastrichtian	71.3–65
Burgos Basin	middle Eocene	48
El Bosque, La Trinidad	Eocene	
Pie de Vaca	Oligocene	
La Quinta	Oligo–Miocene	24
Pichucalco	early to middle Miocene	
San José del Carmen	middle (?) Miocene	
Palomares	middle (?) Miocene	
Ixtapa	middle to late Miocene	
Mint Canyon	late Miocene	
DSDP 66	Miocene–Holocene	
Paraje Solo	middle Pliocene	3–4
Santa María Amajac	late Pliocene–Pleistocene	4–2
Antilles		
Los Ranchos	Neocomian	132
Horizon A/Cat Island	Middle Cretaceous	
San Adrián	Middle Cretaceous	
Saramaguacán	middle Eocene	48
Guys Hill (Chapelton)	middle Eocene	48
San Sebastián	middle Oligocene	35
Amber inclusions (La Toca, Yanigua formations)	early to middle Miocene	15–20
Artibonite	Mio–Pliocene	5–7
Yumari	Tertiary undifferentiated (Miocene?)	
Sánchez	Tertiary undifferentiated–Pleistocene	
Central America		
Chipaxché	Late Cretaceous	
Gatuncillo	late Eocene	35
Culebra, Cucaracha, La Boca	early Miocene	20
Gatún	late Miocene	10
Padre Miguel	Mio–Pliocene	5–7
Herrería	Pliocene	3–4
Sheroli/Sixaola/Río Banano	Pliocene	3–4
Zent/Río Banano	Pliocene	3–4
Cuscatlán/Sisimico–Tal	Plio–Pleistocene	2–3

would almost certainly result in a larger precipitation decrease than that predicted by CLIMAP."

A core from the Darién (Cana Swamp; 7°45'N, 77°35'W) covering the past 4000 years shows some evidence of climate-induced vegetation changes, but as interpreted these do not correlate with other regional changes, and they are ascribed to local events. The spore and pollen profile reveals a record of modest human disturbance and forest recovery in a "remote region rich in endemic species and purported to be one of the last untouched Neotropical wildernesses" (Bush & Colinvaux, 1994). The sediments contain pollen of *Zea* (2%), pollen of disturbance taxa (*Cecropia*, *Pilea*, *Trema*), and charcoal fragments, but pollen of forest tree taxa is also present (*Anacardium* type, *Bursera*, *Daphnopsis*, *Didymopanax*, *Ilex*, *Iriartea*, *Mabea*, *Mortoniodendron*, *Ochroma*, *Socratea*). There were certainly some effects of human occupation on lowland vegetation in the Darién during the past 4000 years, and elsewhere in Central America during the past 11,000 years, but it is difficult to accurately estimate the effect.

Another site in Panama is a coastal swamp near Changuinola in Bocas del Toro Province (9°20'N, 82°20'W; Phillips et al., 1997). The study concerns primarily the history of peat formation on the Caribbean coast over the past 4000 years, but the palynological technique used to reconstruct the development of the deposits also provides information of paleoenvironmental interest. An inventory was made of the seven modern peat-forming communities—*Rhizophora mangle* swamp, mixed black-mangrove swamp, *Raphia taedigera* palm swamp, mixed forest swamp, *Campnosperma panamense* forest swamp, sawgrass ± stunted forest swamp, and *Myrica–Cyrilla* bog plain. Pollen was extracted from surface sediments to establish a spore and pollen signature for each community, and the information was used to interpret the microfossil record from two cores. The succession began as a freshwater lagoon palm swamp (*Raphia taedigera*), and was followed by hardwood forest swamp (*Camp-*

nosperma panamense), and eventually a bog plain (*Myrica–Cyrilla*). The organic sediments accumulated in a coastal tropical environment and formed peat (and will form Tertiary lignites and coal). *Rhizophora* pollen was not preserved here because, in the zone represented by the peat samples, other brackish water plants were dominant—in this case, the multiple-stemmed and pneumatophore-forming, brackish to freshwater palm *Raphia taedigera*. In the Caribbean region, before the arrival of *Rhizophora* at the beginning of the late Eocene, the mangrove habitat was occupied by the Old World palm *Nypa*, *Pelliceria*, *Acrostichum*, and by a plant of unknown biological affinities with *Brevitricolpites variabilis* pollen. The record of mangrove habitats in the Caribbean region after the middle Eocene, based on *Rhizophora*, records the minimum extent because, as shown at Changuinola, some sites were probably occupied by other mangroves. The profile also shows alterations in vegetation attributable to succession rather than to climate.

In Chapter 4, the Younger Dryas (~12–11 Kyr B.P.) and other events were documented to about ~17°N (Yucatán Peninsula). In the Antilles (Chapter 5), waters off the coast of Puerto Rico (~17°N) were slightly cooler at the time of the Little Ice Age (1300–850 C.E.), and in Central America (Chapter 6) effects of the Younger Dryas may have extended to Guatemala (Lake Quexil, ~17°N). In Costa Rica (La Chonta, Lachner bogs, Cerro Chirripó) and Gatún Lake, Panama, they are documented to ~9°S. The Gatún assemblages also suggest slight warming (by ~1° C) during the PGCO or mid-Holocene warm period (~8000–6000 years B.P.) at this latitude. One use of Quaternary plant studies in South America will be to continue assessing evidence for the Younger Dryas and other events in the Northern Andes, across the transition zone of the Central Andes, and into the southernmost latitudes (Chapter 7).

REFERENCES

Anchukaitis, K. J. and S. P. Horn. 2005. A 2000-year reconstruction of forest disturbance from southern Pacific Costa Rica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 221: 35–54.

Anselmetti, F. S. et al. (+ 7 authors). 2006. Late Quaternary climate-induced lake level variations in Late Petén Itzá, Guatemala, inferred from seismic stratigraphic analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 230: 52–69.

Bartlett, A. S. and E. S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change). *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 203–299.

Berry, E. W. 1914. Fossil plants in the Panama Canal Zone. Science 38: 357.

———. 1918. The fossil higher plants from the Canal Zone. *In:* Contributions to the Geology and Paleontology of the Canal Zone, Panama, and Geologically Related Areas in Central America and the West Indies. Bull. U.S. Natl. Mus. 103: 15–44.

———. 1921a. Tertiary fossil plants from Costa Rica. Proc. U. S. Natl. Mus. 59: 169–185.

———. 1921b. A palm nut from the Miocene of the Canal Zone. Proc. U. S. Natl. Mus. 59: 21–22.

———. 1928. A palm fruit from the Miocene of western Panama. J. Wash. Acad. Sci. 18: 455–457.

Bird, J. and R. Cooke. 1978. The occurrence in Panama of two types of Paleo-Indian projectile points. *In:* A. Bryan (ed.), Early Man in America from a Circum–Caribbean Perspective. Occasional Papers Number 1, Department of Anthropology, University of Alberta, Edmonton, Alberta. pp. 263–272.

Bottazzi, G., J. A. Fernandez, and G. Barboza. 1994. Sedimentología e historia tectono-sedimentaria de la cuenca Limón sur. Profil (Institut für Geologie und Paläontologie, Universität Stuttgart) 7: 351–391.

Brown, R. W. 1947. Fossil plants and human footprints in Nicaragua. J. Paleontol. 21: 38–40.

Budd, A. F., K. G. Johnson, T. A. Stemann, and B. H. Tomkins. 1999. Pliocene to Pleistocene reef coral assemblages in the Limón Group of Costa Rica. *In:* L. S. Collins and A. G. Coates (eds.), A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama. Bull. Amer. Paleontol. 357: 119–158.

Bush, M. B. and P. A. Colinvaux. 1990. A pollen record of a complete glacial cycle from lowland Panama. J. Veg. Sci. 1: 105–118.

——— and ———. 1994. Tropical forest disturbance: Paleoecological records from Darién, Panama. Ecology 75: 1761–1768.

——— et al. (+ 6 authors). 1992. A 14,300-yr paleoecological profile of a lowland tropical lake in Panama. Ecol. Monogr. 62: 251–275.

Cassell, D. T. and B. K. Sen Gupta. 1989a. Pliocene foraminifera and environments, Limón Basin of Costa Rica. J. Paleontol. 63: 146–157.

——— and ———. 1989b. Foraminiferal stratigraphy and paleo-environments of the Tertiary Uscari Formation, Limón Basin, Costa Rica. J. Foraminiferal Res. 19: 52–71.

Clement, R. M. and S. P. Horn. 2001. Pre-Columbian land-use history in Costa Rica: A 3000-year record of forest clearance, agriculture and fires from Laguna Zoncho. The Holocene 11: 419–426.

Cole, W. S. 1952. Eocene and Oligocene larger foraminifera from the Panama Canal Zone and vicinity. U.S. Geol. Surv. Prof. Paper 244: 1–41.

Colinvaux, P. 1993. Pleistocene biogeography and diversity in tropical forests of South America. *In:* P. Goldblatt (ed.), Biological Relationships between Africa and South America. Yale University Press, New Haven, CT. pp. 473–499.

Collins, L. S. and A. G. Coates (eds.). 1999. A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama. Bull. Amer. Paleontol. No. 357: 5–351.

Cooke, C. W., J. A. Gardner, and W. P. Woodring. 1943. Cor-

relation of the Cenozoic formations of the Atlantic and Gulf Coastal Plain and the Caribbean region. Geol. Soc. Amer. Bull. 54: 1713–1723.

Cooke, R. 1998. Human settlement of Central America and northernmost South America (14,000–8000 B.P.). Quatern. Int. 49/50: 177–190.

Curtis, J. H. et al. (+ 5 authors). 1998. A multi-proxy study of Holocene environmental change in the Maya lowlands of Petén, Guatemala. J. Paleolimnol. 19: 139–159.

Deevey, E. S., Jr. 1978. Holocene forests and Maya disturbance near Quexil Lake, Petén, Guatemala. Polsk. Arch. Hydrobiol. 25: 117–129.

Dettmann, M. E. and H. T. Clifford. 1992. Phylogeny and biogeography of *Ruffordia*, *Mohria* and *Anemia* (Schizaeaceae) and *Ceratopteris* (Pteridaceae): Evidence from *in situ* and dispersed spores. Alcheringa 16: 269–314.

Donnelly, T. W., G. S. Horne, R. C. Finch, and E. López-Ramos. 1990. Northern Central America; the Maya and Chortis blocks. *In:* G. Dengo and J. E. Case (eds.), The Caribbean Region. Geological Society of America, Boulder, CO. pp. 37–76.

Dowsett, H. J. and T. M. Cronin. 1990. High eustatic sea level during the middle Pliocene: Evidence from the southeastern U.S. Atlantic Coastal Plain; with suppl. data 90–13. Geology 18: 435–438.

——— et al. (+ 8 authors). 1994. Joint investigations of middle Pliocene climate, I, PRISM paleoenvironmental reconstructions. Global Planet. Change 9: 169–195.

——— et al. (+ 6 authors). 1999. Middle Pliocene paleoenvironmental reconstruction: PRISM2. U.S. Geol. Surv. Open File report 99–535.

Driese, S. G., K. H. Orvis, S. P. Horn, Z.-H. Li, and D. S. Jennings. 2007. Paleosol evidence for Quaternary uplift and for climate and ecosystem changes in the Cordillera de Talamanca, Costa Rica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 248: 1–23.

Dull, R. A. 2004. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. Quatern. Res. 61: 159–167.

Dunning, N., D. J. Rue, T. Beach, A. Covich, and A. Traverse. 1998. Human-environment interactions in a tropical watershed: The paleoecology of Laguna Tamarindito, El Petén, Guatemala. J. Field Archaeol. 25: 139–151.

Gentry, A. H. 1985. Contrasting phytogeographic patterns of upland and lowland Panamanian plants. *In:* W. G. D'Arcy and M. D. Correa A. (eds.), The Botany and Natural History of Panama. Monogr. Syst. Bot. Missouri Bot. Gard. 10: 147–160.

Gómez, L. D. 1970. A first report of fossil fern-like Pteropsida from Costa Rica. Rev. Biol. Trop. 16: 255–258.

———. 1971. *Palmacites berryanum*, a new palm fossil from the Costa Rican Tertiary. Rev. Biol. Trop. 19: 121–132.

———. 1972. *Karatophyllum bromelioides* L. D. Gómez (Bromeliaceae), nov. gen. et sp., del Terciario medio de Costa Rica. Rev. Biol. Trop. 20: 221–229.

———. 1973. Criptonemiales calcáreas fósiles en las calizas Tertiarias de Patarrá, Costa Rica. Rev. Biol. Trop. 21: 107–110.

Graham, A. 1977. New records of *Pelliceria* (Theaceae/Pelliceriaceae) in the Tertiary of the Caribbean. Biotropica 9: 48–52.

———. 1979. *Mortoniodendron* (Tiliaceae) and *Sphaeropteris*/*Trichipteris* (Cyatheaceae) in Cenozoic deposits of the Gulf-Caribbean region. Ann. Missouri Bot. Gard. 66: 572–576.

———. 1980. Morfología del polen de *Eugenia*/*Myrcia* (Myrtaceae) y *Combretum*/*Terminalia* (Combretaceae) en relación a su alcance estratigráfico en el Terciario del Caribe. Biotica 5: 5–14.

———. 1984. *Lisianthus* pollen from the Eocene of Panama. Ann. Missouri Bot. Gard. 71: 987–993.

———. 1985. Studies in Neotropical paleobotany. IV. The Eocene communities of Panama. Ann. Missouri Bot. Gard. 72: 504–534.

———. 1987a. Miocene communities and paleoenvironments of southern Costa Rica. Amer. J. Bot. 74: 1501–1518.

———. 1987b. Fossil pollen of *Sabicea* (Rubiaceae) from the lower Miocene Culebra Formation of Panama. Ann. Missouri Bot. Gard. 74: 868–870.

———. 1987c. Tropical American Tertiary floras and paleoenvironments: Mexico, Costa Rica, and Panama. Amer. J. Bot. 74: 1519–1531.

———. 1988a. Studies in Neotropical paleobotany. V. The lower Miocene communities of Panama—The Culebra Formation. Ann. Missouri Bot. Gard. 75: 1440–1466.

———. 1988b. Studies in Neotropical paleobotany. VI. The lower Miocene communities of Panama—The Cucaracha Formation. Ann. Missouri Bot. Gard. 75: 1467–1479.

———. 1989. Studies in Neotropical paleobotany. VII. The lower Miocene communities of Panama—The La Boca Formation. Ann. Missouri Bot. Gard. 76: 50–66.

———. 1990. New angiosperm records from the Caribbean Tertiary. Amer. J. Bot. 77: 897–910.

———. 1991a. Studies in Neotropical paleobotany. VIII. The Pliocene communities of Panama—Introduction and ferns, gymnosperms, angiosperms (monocots). Ann. Missouri Bot. Gard. 78: 190–200.

———. 1991b. Studies in Neotropical paleobotany. IX. The Pliocene communities of Panama—angiosperms (dicots). Ann. Missouri Bot. Gard. 78: 201–223.

———. 1991c. Studies in Neotropical paleobotany. X. The Pliocene communities of Panama—Composition, numerical representations, and paleocommunity paleoenvironmental reconstructions. Ann. Missouri Bot. Gard. 78: 465–475.

———. 1995. Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. Biotropica 27: 20–27.

———. 1998. Studies in Neotropical paleobotany. XI. Late Tertiary vegetation and environments of southeastern

Guatemala: Palynofloras from the Mio–Pliocene Padre Miguel Group and the Pliocene Herrería Formation. Amer. J. Bot. 85: 1409–1425.

———. 2001. Geología y paleobotánica. *In:* W. D. Stevens, C. Ulloa Ulloa, A. Pool, and O. Montiel (eds.), Flora de Nicaragua. Missouri Botanical Garden Press, St. Louis. pp. 28–29.

———. 2006. The history of the vegetation of Guatemala; Cretaceous and Tertiary. *In:* E. B. Cano (ed.), Biodiversidad de Guatemala. Vol. 1. Universidad del Valle de Guatemala, Guatemala City. pp. 7–14.

——— and D. L. Dilcher. 1998. Studies in Neotropical paleobotany. XII. A palynoflora from the Pliocene Río Banano Formation of Costa Rica and the Neogene vegetation of Mesoamerica. Amer. J. Bot. 85: 1426–1438.

———, R. H. Stewart, and J. L. Stewart. 1985. Studies in Neotropical paleobotany. III. The Tertiary communities of Panama—Geology of the pollen-bearing sediments. Ann. Missouri Bot. Gard. 72: 485–503.

Hansen, B. C. S. 1990. Pollen stratigraphy of Laguna de Cocos. *In:* M. D. Pohl (ed.), Ancient Maya Wetland Agriculture: Excavations on Albion Island, Northern Belize. Westview Press, Boulder, CO. pp. 155–186.

Haug, G. H. et al. (+ 5 authors). 2003. Climate and the collapse of Maya civilization. Science 299: 1731–1735.

Haywood, A. M., P. J. Valdes, J. E. Francis, and B. W. Sellwood. 2002. Global middle Pliocene biome reconstruction: A data/model synthesis. Geochem. Geophys. Geosystems 3: 1–18.

Hooghiemstra, H., A. M. Cleef, G. W. Noldus, and M. Kappelle. 1992. Upper Quaternary vegetation dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). J. Quatern. Sci. 7: 205–225.

Horn, S. P. 1990. Timing of deglaciation in the Cordillera de Talamanca, Costa Rica. Climate Res. 1: 81–83.

——— and L. M. Kennedy. 2001. Pollen evidence of maize cultivation 2700 B.P. at La Selva Biological Station, Costa Rica. Biotropica 33: 191–196.

——— and B. L. League. 2005. Registros de sedimentos lacustres de la vegetación del Holoceno e historia del fuego en el páramo de Costa Rica. *In:* L. M. Kappelle and S. P. Horn (eds.), Páramos de Costa Rica. Editorial INBio, Santo Domingo de Heredia, Costa Rica. pp. 253–273.

——— and W. Ramirez B. 1990. On the occurrence of *Ficus* pollen in Neotropical Quaternary sediments. Palynology 14: 3–6.

Hutchinson, G. E. and C. E. Goulden. 1966. The plant microfossils. *In:* U. M. Cowgill et al. (+ 5 authors), The History of Laguna de Petenxil, a Small Lake in Northern Guatemala. Mem. Connecticut Acad. Arts 17. pp. 67–73.

Islebe, G. A. 1996. Vegetation, Phytogeography and Paleoecology of the Last 20,000 Years of Montane Central America. University of Amsterdam, Amsterdam.

——— and H. Hooghiemstra. 1995. Recent pollen spectra of highland Guatemala. J. Biogeogr. 22: 1091–1099.

——— and ———. 1997. Vegetation and climate history of montane Costa Rica since the last glacial. Quatern. Sci. Rev. 16: 589–604.

———, ———, and K. van der Borg. 1995. A cooling event during the Younger Dryas Chron in Costa Rica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117: 73–80.

———, ———, and R. van't Veer. 1996a. Holocene vegetation and water level history in two bogs of the Cordillera de Talamanca, Costa Rica. Vegetatio 124: 155–171.

——— and B. Leyden. 2006. La vegetación de Guatemala durante el Pleistoceno terminal y Holoceno. *In:* E. B. Cano (ed.), Biodiversidad de Guatemala. Universidad del Valle de Guatemala, Guatemala City. pp. 15–23.

——— et al. (+ 5 authors). 1996b. A Holocene vegetation history of lowland Guatemala. *In:* G. A. Islebe (ed.), Vegetation, Phytogeography and Paleo-ecology of the Last 20,000 years of Montane Central America. University of Amsterdam, Amsterdam. pp. 81–99.

Jacob, J. S. and C. T. Hallmark. 1996. Holocene stratigraphy of Cobweb Swamp, a Maya wetland in northern Belize. Geol. Soc. Amer. Bull. 108: 883–891.

Kappelle, M. 1996. Los Bosques de Roble (*Quercus*) de la Cordillera de Talamanca, Costa Rica, Biodiversidad, Ecología, Conservatión y Desarrollo. University of Amsterdam, Amsterdam.

———, A. M. Cleef, and A. Chaverri. 1989. Phytosociology of the montane *Chusquea–Quercus* forests, Cordillera de Talamanca, Costa Rica. Brenesia 32: 73–105.

———, J. G. van Uffelen, and A. M. Cleef. 1995. Altitudinal zonation of montane *Quercus* forests along two transects in the Chirripó National Park, Costa Rica. Vegetatio 119: 119–153.

Kennedy, L. M. and S. P. Horn. 1997. Prehistoric maize cultivation at the La Selva Biological Station, Costa Rica. Biotropica 29: 368–370.

Kesel, R. H. 1983. Quaternary history of the Río General Valley, Costa Rica. Res. Rep. Natl. Geogr. Soc. 15: 339–358.

Krantz, D. E. 1991. A chronology of Pliocene sea-level fluctuations: The U.S. middle Atlantic Coastal Plain record. *In:* T. M. Cronin and H. J. Dowsett (eds.), Pliocene Climates. Quatern. Sci. Rev. 10: 163–174.

Lachniet, M. S. and L. Vázquez-Selem. 2005. Last glacial maximum equilibrium line altitudes in the circum-Caribbean (Mexico, Guatemala, Costa Rica, Colombia, and Venezuela). Quatern. Int. 138/139: 129–144.

Leyden, B. W. 1984. Guatemalan forest synthesis after Pleistocene aridity. Proc. Natl. Acad. Sci. U.S.A. 81: 4856–4859.

———. 1985. Late Quaternary aridity and Holocene moisture fluctuations in the Lake Valencia Basin, Venezuela. Ecology 66: 1279–1295.

———. 1987. Man and climate in the Maya lowlands. Quatern. Res. 28: 407–414.

———. 1995. Evidence of the Younger Dryas in Central

America. Quatern. Sci. Rev. 14: 833–839.

———. 2002. Pollen evidence for climatic variability and cultural disturbance in the Maya lowlands. Ancient Mesoamerica 13: 85–101.

———, M. Brenner, D. A. Hodell, and J. H. Curtis. 1993. Late Pleistocene climate in the Central American lowlands. *In:* P. K. Swart, K. C. Lohmann, J. McKenzie, and S. Savin (eds.), Climate Change in Continental Isotopic Records. Geophys. Monogr. 78: 165–178.

———, ———, ———, and ———. 1994. Orbital and internal forcing of climate on the Yucatán Peninsula for the past ca. 36 ka. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 193–210.

Lötschert, W. and K. Mädler. 1975. Die Plio–Pleistozäne flora aus dem Sisimico–Tal, El Salvador. Geol. Jahrb. 13: 97–191.

Lozano-Garcia, M. S. and B. Ortega-Guerrero. 1994. Palynological and magnetic susceptibility records of Lake Chalco, central Mexico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 177–191.

Martin, P. S. 1960. Effect of Pleistocene climatic change on biotic zones near the equator. Yearb. Amer. Philos. Soc. 1960: 265–267.

———. 1961. Paleoclimatology and a tropical pollen profile. Report VIth Internat. Congr. Quaternary, Warsaw, 1961 (Vol. 2): 319–323. [Proceedings, 1964.]

McNeill, D. F., A. G. Coates, A. F. Budd, and P. F. Borne. 2000. Integrated paleontologic and paleomagnetic stratigraphy of the upper Neogene deposits around Limón, Costa Rica: A coastal emergence record of the Central American Isthmus. Geol. Soc. Amer. Bull. 112: 963–981.

Northrop, L. A. and S. P. Horn. 1996. PreColumbian agriculture and forest disturbance in Costa Rica: Palaeoecological evidence from two lowland rainforest lakes. The Holocene 6: 289–299.

Orvis, K. H. and S. P. Horn. 2000. Quaternary glaciers and climate on Cerro Chirripó, Costa Rica. Quatern. Res. 54: 24–37.

Phillips, S., G. E. Rouse, and R. M. Bustin. 1997. Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panamá. Palaeogeogr. Palaeoclimatol. Palaeoecol. 128: 301–338.

Piperno, D. R. 2006. Quaternary environmental history and agricultural impact on vegetation in Central America. *In:* A. Graham (ed.), Latin American Biogeography—Causes and Effects. Ann. Missouri Bot. Gard. 93: 274–296.

———, M. B. Bush, and P. A. Colinvaux. 1990. Paleoenvironments and human settlement in late-glacial Panama. Quatern. Res. 33: 108–116.

———, ———, and ———. 1991a. Paleoecological perspectives on human adaptation in Central Panama. I. The Pleistocene. Geoarchaeology 6: 201–226.

———, ———, and ———. 1991b. Paleoecological perspectives on human adaptations in Central Panama. II. The Holocene. Geoarchaeology 6: 227–250.

———, K. Husum-Clary, R. G. Cooke, A. J. Ranere, and D. Weiland. 1985. Preceramic maize in central Panama: Evidence from phytoliths and pollen. Amer. Anthropol. 87: 871–878.

——— and D. M. Pearsall. 1998. The Origins of Agriculture in the Lowland Neotropics. Academic Press, New York.

———, A. J. Ranere, I. Holst, and P. Hansell. 2000. Starch grains reveal early root crop horticulture in the Panamian tropical forest. Nature 407: 894–897.

Rodgers, J. C. III, and S. P. Horn. 1996. Modern pollen spectra from Costa Rica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 124: 53–71.

Rosenmeier, M. F., D. A. Hodell, M. Brenner, and J. H. Curtis. 2002. A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Petén, Guatemala. Quatern. Res. 57: 183–190.

Snarskis, M. J. 1981. The archaeology of Costa Rica. *In:* S. Abel-Vidor et al. (+ 11 eds.), Between Continents/Between Seas: Precolumbian Art of Costa Rica. Harry N. Abrams, New York. pp. 15–84.

Stephenson, L. W. and E. W. Berry. 1929. Marine shells in association with land plants in the Upper Cretaceous of Guatemala. J. Paleontol. 3: 157–162.

Stewart, R. H. and J. L. Stewart (with the collaboration of W. P. Woodring). 1980. Geologic Map of the Panama Canal and Vicinity, Republic of Panama. Scale 1:100,000. U.S. Geol Surv. Misc. Invest. Map I-1232. [Map also included in Woodring, 1982, U.S. Geol. Surv. Prof. Paper 306F.]

Stute, M. et al. (+ 7 authors). 1995. Cooling of tropical Brazil (5° C) during the last glacial maximum. Science 269: 379–383.

Tryon, R. M. and A. F. Tryon. 1982. Ferns and Allied Plants with Special Reference to Tropical America. Springer Verlag, Berlin.

Tsukada, M. 1966. The pollen sequence. *In:* U. M. Cowgill et al. (+ 5 authors), The History of Laguna de Petenxil, a Small Lake in Northern Guatemala. Mem. Connecticut Acad. Arts 17. pp. 63–66.

——— and E. S. Deevey Jr. 1967. Pollen analyses from four lakes in the southern Maya area of Guatemala and El Salvador. *In:* E. J. Cushing and H. E. Wright (eds.), Quaternary Paleoecology. Yale University Press, New Haven, CT. pp. 303–331.

van der Hammen, T. and M. L. Absy. 1994. Amazonia during the Last Glacial. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 247–261.

Vaughan, H. H., E. S. Deevey Jr., and S. E. Garrett-Jones. 1985. Pollen stratigraphy of two cores from the Petén Lake District, with an appendix on two deep-water cores. *In:* M. D. Pohl (ed.), Prehistoric Lowland Maya Environment and Subsistence Economy. Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA. pp. 73–89.

Vokes, E. H. 1983. Additions to the Typhinae (Gastropoda: Muricidae) of the Gatún Formation, Panama. Tulane

Studies Geol. Paleontol. 17: 123–130.
Whitmore, T. C. and G. T. Prance (eds.). 1987. Biogeography and Quaternary History in Tropical America. Oxford Science Publications, Oxford, U.K.
Wiseman, F. M. 1983. Analysis of pollen from the fields at Pulltrouser Swamp. *In:* B. L. Turner II and P. D. Harrison (eds.), Pulltrouser Swamp: Ancient Maya Habitat, Agriculture, and Settlement in Northern Belize. University of Texas Press, Austin. pp. 105–119.
Woodring, W. P. 1957–1982. Geology and paleontology of the Canal Zone and adjoining parts of Panama. U.S. Geol. Surv. Prof. Paper 3306A–F.
Wooller, M. J., H. Behling, B. J. Smallwood, and M. Fogel. 2004. Mangrove ecosystem dynamics and elemental cycling at Twin Cays, Belize, during the Holocene. J. Quatern. Sci. 19: 703–711.
Zachos, J. C. et al. (+ 7 authors). 2003. A transient rise in tropical sea surface temperature during the Paleocene–Eocene thermal maximum. Science 302: 1551–1554.

ADDITIONAL REFERENCES/GENERAL READINGS

Prehistoric Fires

Horn, S. P. 1989. Prehistoric fires in the Chirripó highlands of Costa Rica: Sedimentary charcoal evidence. Rev. Biol. Trop. 37: 139–148.
———. 1992. Holocene fires in Costa Rica. Biotropica 24: 354–361.
———. 1993. Postglacial vegetation and fire history in the Chirripó páramo of Costa Rica. Quatern. Res. 40: 107–116.
——— and R. L. Sanford Jr. 1998. Ancient fires and fields: Reconstructing the long-term biotic history of the Las Cruces area. Amigos Newslett. 50: 12–15.
League, B. and S. P. Horn. 2000. A 10,000 year record of páramo fires in Costa Rica. J. Trop. Ecol. 16: 747–752.

Other References/Readings

Bawaya, M. 2005. Maya archaeologists turn to the living to help save the dead. Science 309: 1317–1318. [To preserve ancient sites, pioneering archaeologists are trying to improve the lives of the Maya people now living near the ruins.]
Cano, E. B. (ed.) 2006. Biodiversidad de Guatemala. Universidad del Valle de Guatemala, Guatemala City.
Cohen, A. D., R. Raymond Jr., S. Mora, A. Alverado, and L. Malavassi. 1985. Economic characterization of the peat deposits of Costa Rica, preliminary study. *In:* B. Wade (ed.), Tropical Peat Resources, Prospects and Potential. International Peat Society, Helsinki. pp. 146–169.
———, ———, A. Ramirez, Z. Morales, and F. Ponce. 1989. The Changuiola peat deposit of northwestern Panama: A tropical back-barrier peat (coal)-forming environment. *In:* P. C. Lyons and B. Alpern (eds.), Peat and Coal: Origin, Facies and Depositional Environments. Int. J. Coal Geol. 12: 157–192.
——— and E. M. Stack. 1996. Some observations regarding the potential effects of doming of tropical peat deposits on the composition of coal beds. Int. J. Coal Geol. 29: 39–65.
Cowgill, U. M. et al. (+ 5 authors). 1966. The History of Laguna de Petenxil, a Small Lake in Northern Guatemala. Mem. Connecticut Acad. Arts 17: 1–126.
Enquist, C. A. F. 2002. Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. J. Biogeogr. 29: 519–534.
Haberyan, K. A. and S. P. Horn. 1999. A 10,000 year diatom record from a glacial lake in Costa Rica. Mountain Res. Developm. 19: 63–70.
Horn, S. P. 1985. Preliminary pollen analysis of Quaternary sediments from Deep Sea Drilling Project site 565, western Costa Rica. Initial Reports of the Deep Sea Drilling Project 84: 533–547.
———. 1986. Key to the Quaternary pollen of Costa Rica. Brenesia 25/26: 33–44.
———. 1992. Microfossils and forest history in Costa Rica. *In:* H. K. Steen and R. P. Tucker (eds.), Changing Tropical Forests: Historical Perspectives on Today's Challenges in Central and South America. Forest History Society, Durham, NC. pp. 16–30.
———, K. H. Orvis, and K. A. Haberyan. 1999. Investigación limnológica y geomorfológica de lagos glaciares del Parque Nacional Chirripó, Costa Rica. Revista Informe Semestral 35: 95–106.
——— and J. C. Rogers III. 1996–1997. The northern limit of *Alnus* (Fagales) in Costa Rica: Modern pollen evidence of a possible range extension. Rev. Biol. Trop. 44/45: 609–611.
Kirby, M. X. and B. MacFadden. 2005. Was southern Central America an archipelago or a peninsula in the middle Miocene? A test using land-mammal body size. Palaeogeogr. Palaeoclimatol. Palaeoecol. 228: 193–202.
Leduc, G. et al. (+ 6 authors). 2007. Moisture transport across Central America as a positive feedback on abrupt climatic changes. Nature 445: 908–911.
Lewin, R. 1984. Fragile forests implied by Pleistocene pollen. Science 226: 36–37. [Summary of Leyden, 1984 paper.]
MacFadden, B. J. 2006. Extinct mammalian biodiversity of the ancient New World tropics. Trends Ecol. Evol. 21: 157–165.
Massot, T. W. 1987. The coal potential of Bocas del Toro, Panama. Reconnaissance Report (Mimeographed), BHP/Utah Minerals International, Herndon, VA.
Miksicek, C. H. et al. (+ 5 authors). 1981. Preclassic lowland maize from Cuello, Belize. Nature 289: 56–59.
Pearson, G. A. 2005. Late Pleistocene megafaunal deposits on the Isthmus of Panama and their paleoenvironmental implications. Caribbean J. Sci. 41: 1–13.
Peres, C. A., J. Barlow, and W. F. Laurance. 2006. Detecting anthropogenic disturbances in tropical forests. Trends Ecol. Evol. 21: 227–229.

Perry, L. (+ 14 authors). 2007. Starch fossils and the domestication and dispersal of chili peppers (*Capsicum* spp. L.) in the Americas. Science 315: 986–988. [See also p. 909.]

Piperno, D. R., E. Weiss, I. Holst, and D. Nadel. 2004. Processing of wild cereal grains in the upper Paleolithic revealed by starch grain analysis. Nature 430: 670–673.

Retallack, G. J. and M. X. Kirby. 2007. Middle Miocene global change and paleogeography of Panama. Palaios 22: 667–679. [Cucaracha time: "…a mosaic of swamp to mangal (mangrove forests) preserving plants and dry uplands preserving mammals."]

Sanchez, J. D., J. P. Bradbury, B. F. Bohor, and D. A. Coates. 1987. Diatoms and tonsteins as paleoenvironmental and paleodepositional indicators in a Miocene coal bed, Costa Rica. Palaios 2: 158–164.

Umaña Villalobos, G., K. A. Haberyan, and S. P. Horn. 1999. Limnology in Costa Rica. Limnol. Developing Countries 2: 33–62.

Chapter 7

SOUTH AMERICA

Cautionary notes and opinions 2 (Identifications):

Romero and Arguijo (1981a) reviewed early publications on floras spanning the Late Cretaceous to the Eocene of southern South America. Taxa present, and not unexpected in the Maastrichtian, were *Hymenophyllum* (Hymenophyllaceae), *Acmopyle* (Podocarpaceae–Taxaceae), *Podocarpus* (Podocarpaceae), and *Cinnamomum* (Lauraceae), and in the Paleogene *Hydrangea*(?) (Hydrangeaceae), *Laurelia* (Atherospermataceae–Lauraceae–Monimiaceae), *Peumus* (Monimiaceae), and *Sterculia* (Sterculiaceae). Unexpected for the Cretaceous of southern South America were *Myrica* (Myricaceae), *Platanus* (Platanaceae), *Populus* (Salicaceae), *Quercus* (Fagaceae), *Salix* (Salicaceae), and *Liquidambar* (Hamamelidaceae). The latter fossil leaf is similar to one recently compared to the Malvales by Wilf et al. (2003, fig. J). In a more recent summary (Romero, 1993), these northern temperate elements are not mentioned for the Cretaceous and Paleogene.

An awareness of geologic events, trends in climate and paleovegetation, and the phylogenetic position of taxa is useful when considering new contributions to the paleobotanical database, and for evaluating those already in the literature. The geological context for the Middle to Late Cretaceous through the Paleogene of South America includes sea levels higher than at present by up to ~300 m, with all the climatic and physiographic consequences this implies; warm but gradually declining temperatures from mid-Cretaceous highs; the asteroid impact at the end of the Cretaceous 65 Ma with a brief and sudden decline in temperatures; a rise in global MAT to the PETM near 55 Ma; a drop in MAT after that time, marking the transition from a greenhouse to an icehouse world; continuity of land surfaces and prevailing mild climates through southern South America, Antarctica, and Australasia until Australia began separating from Antarctica in the Eocene ~49 Ma, and South America from Antarctica by formation of the Drake Passage near the Eocene–Oligocene boundary ~35 Ma; moderate physiography and habitat diversity until the principal period of High Andean orogeny beginning in the Miocene ~23 Ma; increasing seasonality at ~20 Ma; and South America existing as an island continent from ~35 Ma until connection with North America across the isthmian region at ~3.5 Ma.

The global paleobotanical context includes replacement of the Jurassic–Early Cretaceous pteridophyte-gymnosperm–dominated vegetation beginning in about the Middle Cretaceous by one with a more prominent angiosperm component; fossils (especially pollen) mostly without modern generic analogs through the early Eocene; a noticeable increase in fossils that can be identified to modern genera beginning in about the middle Eocene; and communities mostly without modern formation and association counterparts through the Eocene, with greater similarity developing during the transition times of the Oligocene. These geologic, climatic, and paleobotanical trends impart recognizable stages in the Late Cretaceous and Paleogene development of fossil floras. The expected stages include abundant spores, pollen, and megafossils of pteridophytes and gymnosperms, with angiosperms rare through about the Aptian (121–112 Ma); changes in the Southern Hemisphere at the K/T boundary (65 Ma) possibly attributable to the asteroid impact (extinctions, an increase in the remains of ferns and other colonizing plants, the "fern spike"; see later section); widespread tropical vegetation recognizable by the taxa involved; leaves with features such as large size, entire margins, drip-tips, and thin texture, and wood with no or poorly developed growth rings; increasing distinction between low-latitude (equatorial) and higher-latitude (poleward) vegetation after the early Eocene; a transitional Oligocene vegetation; broad geographical affinities of plants and plant formations because of reduced physical barriers and more equable maritime climates (e.g., through southern South America and Australasia; Cantrill & Nagalingum, 2005); a pre-Miocene vegetation of moderate species and community diversity due, in part, to less habitat diversity in the Andean region, and increasing later; and little evidence of extensive dry and alpine vegetation until late in the Tertiary.

A phylogenetic context is provided by the inferred sequence and time of appearance of various clades based on the synthesis of multi-gene molecular, morphological, and paleobotanical data (e.g., Angiosperm Phylogeny Group, 2009; Soltis & Soltis, 2004; Soltis et al., 2005; review by Crawford, 2006; Fig. 7.1). The plausibility of fossil identifications can be considered within this evolutionary framework. The importance of identifications is highlighted when they place a genus or family near its time of origin or in a new geographic region, and a healthy skepticism should be generated when the taxon is decidedly unexpected given the phylogenetic position of the clade. For example, the Lauraceae (*Laurophyllum*) and possibly the Liliaceae (as *Liliacidites*) are reported from the Cretaceous and Paleocene of several southern South American sites (Table 7.1), and this is not unexpected given their position toward the base of the developing angiosperm phylogeny (Fig. 7.1). The same is true for *Pseudowinterapollis* (= *Drimys*) in the Eocene Sloggett Formation of Tierra del Fuego (Tables 7.1, 7.3).

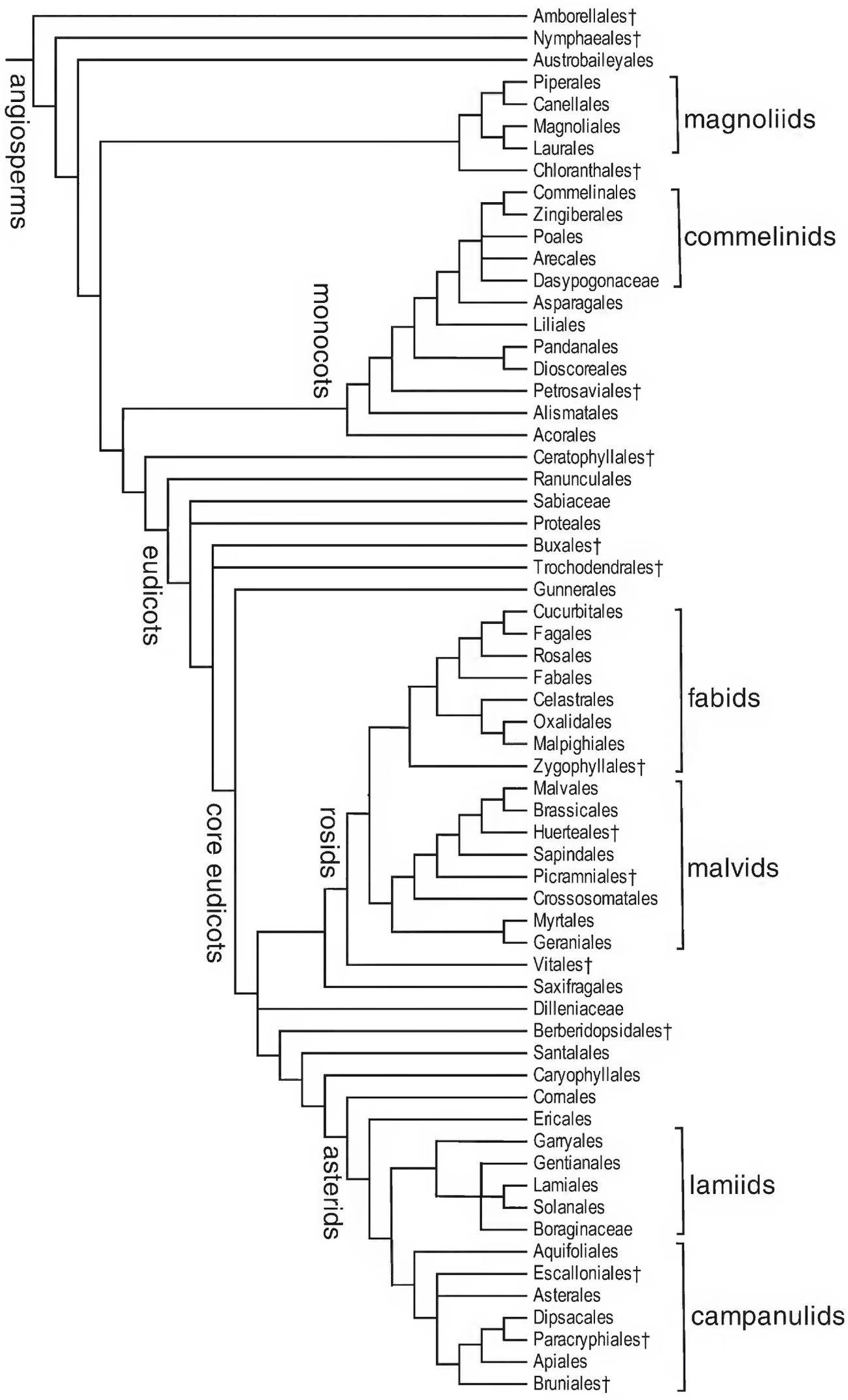


Figure 7.1. Interrelationships of the APG III orders and some families of flowering plants supported by jackknife/bootstrap percentages greater than 50 or Bayesian posterior probabilities greater than 0.95. † = newly recognized orders for APG. From the Angiosperm Phylogeny Group (2009). Used with permission of The Linnean Society of London and Wiley-Blackwell Publishing.

Moderately advanced families of dicotyledon angiosperms include the Amaranthaceae and Chenopodiaceae (Caryophyllales; Jordon & MacPhail, 2003; Furness & Rudall, 2004; Fig. 7.1). The small size of the wind-pollinated grains and their abundance in the atmosphere and in younger sediments make them a potential source of contamination, and some chenoams bear a superficial resemblance to the spherical periporate grains of some Caryophyllaceae (e.g., *Arenaria*, *Stellaria*). Thus, not all reports of the family are certain, especially for the Cretaceous and Paleogene. The oldest record is pollen from the latest Cretaceous of Canada (Muller, 1981). The Amaranthaceae–Chenopodiaceae are not known elsewhere until the Paleocene–Eocene, and not in Australia until the Oligocene. Thus, the report of their occurrence in the Cretaceous–lowermost Paleocene of Buenos Aires Province in Argentina (Ruiz & Quattrocchio, 1997b) is taxonomically and biogeographically important. Another moderately advanced family is the Rhizophoraceae, and the oldest documented fossils are from

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. Unless otherwise indicated, spellings, suggested biological affinities, and age assignments are according to the original authors. Unknowns and specimens designated by an informally applied artificial nomenclature are not included. Unpublished studies are cited in the References but are not included in the Table. Spores and reproductive structures of fungi (e.g., cleistothecia), pyrrophyta (dinoflagellates), diatoms, and other algae are often treated in separate publications, and only those cited in the references below are included here. Refs. = references, as follows, Argentina: 1 = Baldoni and Taylor 1983, 2 = Baldoni and Archangelsky 1983, 3 = Archangelsky et al. 1984, 4 = Archangelsky 2001, 5 = Archangelsky and Gamerro [1965 et seq. in series Estudio Palinológico de la Formación Baqueró (Cretácico), Provincia de Santa Cruz], 6 = Gamerro 1977, 7 = Gamerro 1975, 8 = Romero and Arguijo 1981a, 9 = Passalia et al. 2001, 10 = Archangelsky et al. 1994, 11 = Stough 1968, 12 = Archangelsky and Romero 1974, 13 = Menéndez and Caccavari de Filice 1975, 14 = Berry 1937a, 15 = Hunicken 1955, 16 = Freile 1972, 17 = Papu 1988, 18 = Palamarczuk and Gamerro 1988, 19 = Ruiz and Quattrocchio 1997a, b, Quattrocchio and Ruiz 1999, 20 = Papu 1990, 21 = Archangelsky et al. 1999, 22 = Romero 1968, 23 = Petriella 1969, 24 = Petriella 1972, 25 = Romero and Hickey 1976, 26 = Romero et al. 1988, 27 = Durango de Cabrera and Romero 1988, 28 = Berry 1937b, 29 = Archangelsky 1973, 30 = Archangelsky and Zamaloa 1986, 31 = Quattrocchio et al. 1988, 32 = Quattrocchio and Volkheimer 1988, 33 = Quattrocchio and Volkheimer 1990, 34 = Quattrocchio 1978a, 35 = Quattrocchio 1978b, 36 = Ruiz and Quattrocchio 1993, 37 = Quattrocchio et al. 1997, 38 = Berry 1937c, 39 = Romero 1970, 40 = Romero and Arguijo 1981b, 41 = Berry 1938, 42 = Archangelsky 1972, 43 = Romero 1977, 44 = Romero and Zamaloa 1985, 45 = Romero and Castro 1986, 46 = Olivero et al. 1998, 47 = Zamaloa and Romero 1990, 48 = Menéndez 1960, 49 = Palamarczuk and Barreda 2000, 50 = Prámparo et al. 1996, 51 = Barreda 1997a (San Julián Formation), 52 = Barreda 1996, 1997b, c, d, e (all Chenque Formation); Chile: 53 = Menéndez 1966b, 1972a, b (all Cerro Guido locality, Chile), 54 = Nishida 1981a, b, Nishida and Nishida 1985, Nishida et al. 1989, 1990, 1992 (all petrified wood, mostly outwash specimens, geologic formations mostly unknown, ~Late Cretaceous–Eocene? age), 55 = Takahashi 1978, 56 = Doubinger and Chotin 1975, 57 = Troncoso A. 1992, 58 = Berry 1922a, 59 = Palma-Heldt 1980a, 60 = Cookson and Cranwell 1967, 61 = Palma-Heldt 1983, 62 = Uemura 1990, 63 = Yoshida 1990, 64 = Palma-Heldt 1980b; Bolivia: 65 = Vajda-Santivanez 1999, 66 = Horton et al. 2001; Peru: 67 = Elsik 1964, 68 = Elsik 1966, 69 = Berry 1927, 70 = Berry 1929a, 71 = Berry 1929b; Ecuador: 72 = Berry 1929c; Colombia: 73 = Pons 1971, 74 = Pons 1988, 75 = Berry 1924b, 76 = Berry 1924c, 77 = Berry 1924–25, 78a = Huertas G. 1977, 78b = Pons 1983, 78c = Pons 1984, 78d = Herngreen and Dueñas Jimenez 1990, 79 = Doubinger and Pons 1975, 80 = Solé de Porta 1972, 81 = Dueñas Jimenez 1989, 82 = Solé de Porta 1971, 83 = Doubinger and Pons 1971, 84 = van der Hammen and Garcia de Mutis 1966, 85 = Jaramillo and Dilcher 2001, 86 = González-Guzmán 1967, 87 = Schuler and Doubinger 1970; Venezuela: 88 = Berry 1939a, 89 = Berry 1936a, 90 = Sinanoglu 1983, 91 = Colmenares C. 1988, 92 = Di Giacomo and van Erve 1987; Guianas: 93 = van der Hammen and Burger 1966, 94 = van der Hammen and Wijmstra 1964, 95 = Leidelmeyer 1966, 96 = Wijmstra 1971; Brazil: 97a = Dilcher et al. 2005, 97b = Dolianiti 1955, 98 = Fittipaldi et al. 1989, 99 = De Lima 1982, 100 = Pares Regali et al. 1974. Citations within the table are given in Chapter 7 References.

Argentina

Early Cretaceous

Megafossils

[1, Springhill Formation, a diachronous unit ranging from Berriasian–Valanginian (southeast) to Barremian–Aptian (northwest), Cuenca de Magallanes, Santa Cruz Province]

Gymnosperms: *Otozamites archangelskyi*, *Brachyphyllum mamillare*, *Ptilophyllum angustus*. Angiosperms (late Early Cretaceous, Cunéo & Gandolfo, 2005, see text): *Kachaikenia compuesta*, *Rogersia australis*, *Thorphyllum patagonica*

Microfossils

[2, Springhill Formation, as above]

Ferns and allied groups: *Aequitriradites spinulosus*, *A. verrucosus*, *Baculatisporis* cf. *comaumensis*, *Biretisporites*, *Cicatricosisporites australiensis*, *Contignisporites cooksonii*, *Converrucosisporites*, *Coptospora*, *Cyathidites australis*, *Deltoidospora*, *Densoisporites velatus*, *Dictyophyllidites*, *Duplexisporites*, *Gleicheniidites* aff. *cercinidites*, *Horriditriletes*, *Interulobites triangularis*, *Klukisporites labiatus*, *Lycopodiumsporites austroclavatidites*, *Lygodiumsporites*, *Matonisporites tenuilabratus*, *Muricingulisporis*, *Osmundacidites wellmanii*, *Polypodiidites*, *Reticulatisporites*, *Rotverrucosisporites*, *Sestrosporites*, *Staplinisporites caminus*, *Trilites* cf. *tuberculiformis*, *Trilobosporites*. Gymnosperms: *Alisporites*, *Araucariacites australis*, *Callialasporites trilobatus*, *Classopollis*, *Cycadopites nitidus*, *Gliscopollis*, *Microcachryidites antarcticus*, *Podocarpidites* cf. *ellipticus*, *Vitreisporites pallidus*

[3, well cores, various sites, Early Cretaceous (late Berriasian or Valanginian to early Aptian); see also e.g., Archangelsky & Archangelsky, 2002, 2004]

Ferns and allied groups: *Aequitriradites spinulosus*, *A. verrucosus*, *Antulsporites baculatus*, *Appendicisporites* cf. *stylosus*, *Asterisporites chlonovae*, *Cicatricosisporites australiensis*, *C. hughesii*, *Concavissimisporites*, *Contignisporites cooksonii*, *C. fornicatus*, *Couperisporites complexus*, *Cyatheacidites tectifera*, *Densoisporites corrugatus*, *D. velatus*, *Duplexisporites*, *Foraminisporis dailyi*, *F. microgranulatus*, *F. variornatus*, *F. wonthaggiensis*, *Interulobites distannulatus*, *I. intraverrucatus*, *I. pseudoreticulatus*, *Klukisporites scaberis*, *K. tuberosus*, *Laevigatosporites belfordii*, *Leptolepidites macroverrucosus*, *L.* cf. *proxigranulatus*, *Matonisporites tenuilabratus*, *Muricingulisporis annulatus*, *Polycingulatisporites trabeculatus*, *Rotverrucosisporites*, *Schizaeoisporites*, *Staplinisporites caminus*, *Taurocusporites segmentatus*, *Trilobosporites apiverrucatus*, *T. canadensis*, *T. purverulentus*, *Triporoletes reticulatus*, *Verrucosisporites*. Gymnosperms: *Balmeiopsis limbatus*, *Coptospora striata*, *Cyclusphaera crassa*, *C. patagonica*, *C. psilata*, *C. radiata*. Angiosperms (pollen): *Asterisporites asteroides*, *Clavatipollenites hughesii*. Incertae sedis: *Celyphus rallus*, *Microfasta evansii*, *Schizosporis reticulatus*

Megafossils

[4, Baqueró Group, Santa Cruz Province, Aptian]

Fungi: *Brefeldiellites argentina*, *Microthyriacites baqueroensis*, *Trichopeltinites pulcher*. Ferns and allied groups (Lycopsida): *Auriculozonospora spongiosa*, *Bacutriletes guttula*, *B. triangulatus*, *Carbochonicus carbunculus*, *Erlansonisporites sparsis*, *Horstisporites feruglioi*, *H. iridodea*, *Hughesisporites patagonicus*, *H. rugulatus*, *Minerisporites elegans*, *M. laceratus*, *M. patagonicus*, *Verrutriletes tomtaylori*; (Sphenopsida): *Equisetites*; (ferns): *Baqueroites padulae*, *Cladophlebis antarctica*, *C. browniana*, *C. haiburnensis* var. *rectimarginata*, *C. patagonica*, *C. tripinnata*, *Cyathea cyathifolia*, *Gleichenites*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

argentinica, *G. feruglioi*, *G. san-martinii*, *G. vegagrandis*, *Hausmannia papilio*, *H. patagonica*, *Mesosingeria mucronata*, *M.* (?) *obtusa*, *M. striata* (Archangelsky, 1963b), *Ruffordia goepperti*. Fronds (incertae sedis): *Sphenopteris* cf. *fittonii*, *S.* cf. *goepperti* (Archangelsky, 1964), *S. patagonica*, *S.* (*Onychiopsis*) *psilotoides*. Gymnosperms (Pteridospermales, seed ferns): *Ktalenia circularis* (Taylor & Archangelsky, 1985), *Pachypteris elegans*, *P.*? *patagonica*, *Ruflorinia papillosa*, *R. pilifera*, *R. sierra*. Gymnosperm leaves (incertae sedis): *Nilssonia clarkii*, *Taeniopteris*. Gymnosperms (Cycadales): *Almargemia incrassata*, *Mesodescolea plicata*, *Mesosingeria coriacea*, *M. herbstii*, *M. mucronata*, *M.*? *obtusa*, *M. parva*, *M. striata*, *Pseudoctenis crassa*, *P. dentata*, *P. giganteus*, *P. ornata*, *Sueria elegans*, *S. rectinervis*, *Ticoa harrisii*, *T. lamellata*, *T. magnipinnulata*. Gymnosperms (Bennettitales): *Cycadolepis baqueroensis*, *C. coriacea*, *C. involuta*, *C. lanceolata*, *C. menendezii*, *C. oblonga*, *C. petriellai*, *Dictyozamites areolatus*, *D. grandis*, *D. latifolius*, *D. minusculus*, *Otozamites ornatus*, *O. parviauriculata*, *O. waltonii*, *Pterophyllum trichomatosum*, *Ptilophyllum acutifolium*, *P. hislopii*, *P. longipinnatum*, *Williamsonia bulbiformis*, *W. umbonata*, *Zamites decurrens*, *Z. grandis*. Gymnosperms (Ginkgoales): *Allicospermum patagonicum*, *Ginkgoites ticoensis*, *G. tigrensis*, *Karkenia incurva*. Gymnosperms (Coniferales): *Alkastrobus peltatus*, *Apterocladus lanceolatus*, *Araucaria grandifolia* (Araucariaceae), *Araucarites baqueroensis*, *A. minimus*, *Athrotaxis ungeri*, *Brachyphyllum brettii*, *B. irregulare*, *B. mirandai*, *B. mucronatum*, *B. tigrense* (with *Podocarpidites*-type pollen, Archangelsky & del Fueyo, 1987), *Elatocladus*, *Morenoa fertilis*, *Nothopehuen brevis*, *Podocarpus dubius*, *P.*? *palissyafolia* (Podocarpaceae), *Squamastrobus tigrensis* (Archangelsky & del Fueyo, 1989), *Tarphyderma glabra* (Archangelsky & Taylor, 1986), *Tomaxellia biforme* (with *Classopollis* pollen, Archangelsky, 1968), *T. degiustoi*, *Trisacocladus tigrensis*. Angiosperms (leaves, unidentified; Romero & Archangelsky, 1986). [Kachaike Formation, Santa Cruz, late Aptian to Cenomanian; Longobucco et al., 1985, Aguirre Urreta, 2002, Guler & Archangelsky, 2002; Ferns and allied groups: *Cladophlebis* aff. *haiburnensis* var. *rectimarginata*, *C. patagonica*, *Gleichenites san-martinii*, *Hausmannia papilio*. Gymnosperms: *Pseudoctenis ensiformis*, *Ptilophyllum acutifolium*]

Microfossils

[5, Baqueró Formation, Santa Cruz Province, Aptian]

Ferns and allied groups (some bryophyte spores?): *Aequitriradites baculatus*, *A. spinulosus*, *A. verrucosus*, *Auritulinasporites*, *Baculatisporites comaumensis*, *Biretisporites*, *Calamospora* aff. *mesozoica*, *Camarazonosporites microalveolatus*, *Ceratosporites equalis*, *C. setosus*, *Cibotiidites auriculatus*, *Cicatricosisporites* (*Anemia* fide Dettmann & Clifford, 1992) *annulatus*, *C. australiensis*, *C. baqueroensis*, *C.* cf. *ethmos*, *C. giganteus*, *C. hughesii*, *C. ticoensis*, *Clavifera*, *Concavisporites* cf. *laticrassus*, *Contignisporites cooksonii*, *Coptospora foveolata*, *Cyatheacidites tectifera*, *Cyathidites australis*, *C. minor*, *Deltoidospora minor*, *Densoisporites corrugatus*, *D. velatus*, *Foraminisporis asymmetricus*, *F. dailyi*, *Gleicheniidites senonicus*, *Heliosporites baculatus* [*Antulsporites baculatus*], *Laevigatosporites belfordii*, *L. ovatus*, *Leiotriletes regularis*, *Leptolepidites major*, *Microfoveolatosporis*, *Muricingulisporis annulatus*, *Naiaditaspora gemmata*, *Neoraistrickia*, *Obtusisporis obtusangulus*, *Ornamentifera tuberculata*, *Osmundacidites diazii*, *Polypodiaceoisporites elegans*, *Polypodiidites*, *Reticulatisporites ornatus*, *Retitriletes austroclavatidites*, *R. baqueroense*, *Rotverrucosisporites labratus*, *Rouseisporites reticulatus*, *Rugulatisporites neuquenensis*, *Sestrosporites pseudoalveolatus*, *Staplinisporites caminus*, *Stoverisporites lunaris*, *Taurocusporites segmentatus*, *Trilobosporites apiverrucatus*, *T. purverulentus*, *T. trioreticulosus*, *Tuberculatosporites*, *Vallizonosporites spinosus*, *Verrucosisporites*. Gymnosperms: cf. Podocarpaceae (Archangelsky, 1988)—*Gamerroites psilasaccus*, *G. volkheimeri*; orbiculas (Ubisch bodies from male cones of *Apterocladus lanceolatus*, *Brachyphyllum irregulare*, *Tomaxellia biforme*, and *Trisacocladus tigrensis*; Gamerro, 1968); *Araucariacites* and *Balmeiopsis* (in male cones attached to leafy twigs of *Brachyphyllum*, an extinct Araucariaceae), *Callialasporites* (Podocarpaceae; Archangelsky, 1994); *Cyclusphaera psilata* (gymnosperm–angiosperm ultrastructure features; Taylor et al., 1987). Incertae sedis: *Chomotriletes minor*, *Clavatipollenites* (Archangelsky & Taylor, 1993; angiosperm)

[6, Gorro Frigio Formation, Chubut Province, Patagonia, Aptian]

Ferns and allied groups: *Henrisporites elegans*, *H. musacchioi* (cf. *Isoetes*), *Minerisporites cheblii* (cf. *Isoetes*)

[7, La Amarga Formation, Neuquén Province, Barremian]

Ferns and allied groups: *Favososporites* (*Horstisporites*) *feruglioi*, *F. spinulosus*, *Henrisporites heteracanthus*, *Minerisporites holobrochatus*

Late Cretaceous to Paleogene (Paleocene to Eocene) transition floras, Albian to ~Ypresian, ~112–54.8 Ma

Megafossils

[8, San Jorge and Magallanes basins, Aptian–Turonian, Coniacian, Maastrichtian]

Ferns and allied groups: *Adiantum patagonicum* (Pteridaceae), *Dennstaedtia patagonica* (Dennstaedtiaceae), *Dryopterites problematicus*, *Gleichenites piatnitzkyi*, *Hymenophyllum priscum* (Hymenophyllaceae), *Thyrsopteris antiqua* (Dicksoniaceae). Gymnosperms: *Acmopyle antarctica* (Taxaceae), *Podocarpus inopinatus*, *P. tertiaria* (Podocarpaceae), *Protophyllocladus australis*, *Pseudoaraucaria valentini*. Angiosperms: *Apoci*[*y*]*nophyllum chalianum*, *Aralaephyllum cachetamanense*, *Bignonites chalianum*, *Cinnamomum heeri* (Lauraceae), *Cissites parvifolius*, *Hydrangea* (?) *incerta* (Hydrangeaceae), *Laurelia amarillana* (Antherospermataceae), *Laurophyllum chalianum*, *L. hickenii*, *L. kurtzi*, *L. proteaefolium*, *Liquidambar* [?] *integrifolium* (Hamamelidaceae), *Menispermites obtusiloba*, *M. piatnitzkyi*, *Myrcia acutifolia*, *M. santacruzensis* (Myrtaceae), *Paranymphaea proteaefolia*, *Perseophyllum hauthalianum*, *Peumus clarki*, *Platanus* [?] *obtusiloba* (Platanaceae), *Populites lancastriensis*, *Populus* [?] cf. *nebrascensis*, *P.* cf. *microphylla* (Salicaceae), *Quercus* [?] *primordialis* (Fagaceae), *Rollinia* (?) *patagonica* (Annonaceae), *Ruprechtia castilloensis* (Polygonaceae), *Salix* [?] *proteaefolia* (Salicaceae), *Sassafras* [?] *acutilobum*, *S. cretaceum*, *S. mudgei*, *S. subintegrifolium* (Lauraceae), *Schinopsis* (?) *dubia* (Anacardiaceae), *Sterculia patagonica*, *S. sehuensis*, *S. washburnii* (Sterculiaceae). [Note: the northern temperate genera designated in brackets are not reported in the microfossil flora of the San Jorge Basin (Ref. 10 below).]

[9, Bajo de los Corrales, Santa Cruz Province; Baqueró Group, Chubut Group, Mata Amarilla Formation; Albian; Coniacian in Romero, 1986]

Myrtoidea patagonica, other incertae sedis (see also *Hypocrititriletes insolitus* from an unnamed Middle Cretaceous shale, Río Guanaco, Estancia La Herradura, Santa Cruz Province; Stough, 1968); Romero (1986) adds ferns and allied groups: *Blechnum* (Blechnaceae), *Gleichenia* (Gleicheniaceae), *Hymenophyllum* (Hymenophyllaceae). Gymnosperms: *Dacrydium* (Podocarpaceae), *Podocarpus* (Podocarpaceae). Angiosperms (dicotyledons): *Laurelia* (Monimiaceae)

Microfossils

[10, San Jorge Basin, Caleta Olivia Member, Cañadón Seco Formation, Albian–Cenomanian to early Turonian]

Bryophyta: *Taurocusporites segmentatus*, *Triporoletes reticulatus*. Ferns and allied groups: *Aequitriradites*, *Ceratosporites*, *Cicatricosisporites australiensis*, *C. hughesii*, *C.* sp., *Contignisporites* cf. *cooksonii*, *Crybelosporites*, *Foraminisporis dailyi*, *F. wonthaggiensis*, *Gleicheniidites senonicus*, *Interulobites intraverrucatus*, *I. triangularis*, *Leptolepidites proxigranulatus*, *Matonisporites*, *Nodosisporites*, *Trilobosporites trioreticulosus*, *Verrucosisporites*. Gymnosperms: *Alisporites*, *Callialasporites* cf. *dampieri*, *Classopollis*, *Corollina*, *Cyclusphaera* (?), *Podocarpidites*, *Trisaccites microsaccatum*. Angiosperms: *Clavatipollenites*, *Cupuliferoidaepollenites* cf. *parvulus*, *C.* sp., *Liliacidites*, *Nyssapollenites* cf. *squamosus*, *Phy(i)mopollenites pannosus*, *P.* sp., *Rousea georgensis*, *Tricolpites minutus*, *Verrutricolpites*. Plankton: *Schizosporis reticulatus*

[11, Lago Argentino, Argentina, Mata Amarilla Formation, Middle–Late Cretaceous (Albian)]

Algae?: *Confossia vulgaris*, *C. rara*. Ferns and allied groups: *Ariadnaesporites micromedusus*, *Azolla polyancyra* (Salviniaceae), *Cicatricosisporites*, *Gleicheniidites*. Gymnosperms: *Microcachryidites antarcticus*, *Podosporites microsaccatus*. Angiosperms (?): *Porocolpollenites*, *Rouseisporites*, *Tricesticillus americanus*, *Tricolpites*, *Tricolporites*, *Triporopollenites*; position (?): *Cuparieidites*, *Patera crassa*, *P. tenuis*

[12, Patagonia, Argentina–Chile, Maastrichtian–Paleocene, all gymnosperms, under K in Appendices 2.1, 2.2]

Fortín General Roca, Río Negro Province, Jagüel Formation, middle Maastrichtian: *Podocarpidites microreticuloidata*, *P.* sp. 2; Costa del Estrecho de Magallanes, Magallanes Province (Chile), Río Blanco Formation, late Maastrichtian: *Podocarpidites marwickii*, *P. microreticuloidata*, *P.* sp. 1; Cerro Bororó,

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Chubut Province, Bororó Formation, Danian (basal Paleocene): *Classopollis* sp. 2, *Dacrydiumites florinii*, *Microcachrydites antarcticus*, *Phyllocladidites mawsonii*, *Podocarpidites marwickii*, *P. microreticuloidata*, *P. psilasaccus*, *P.* sp. 1, *Trisaccites microsaccatus*(*m*); Cerro Abigarrado, Chubut Province, Salamanca Formation, Danian: *Araucariacites*, *Classopollis* sp. 1, *Dacrydiumites florinii*, *Microcachrydites antarcticus*, *Phyllocladidites mawsonii*, *Podocarpidites marwickii*, *P.* sp. 1; Bajada de Hansen, Chubut Province, Salamanca Formation, Danian: *Araucariacites*, *Classopollis* sp. 2, *Dacrydiumites florinii*, *Microcachrydites antarcticus*, *Podocarpidites marwickii*, *P.* sp. 1; Cerro Dorotea Formation, Maastrichtian to Danian (Freile, 1972): *Dacrydiumites florinii*, *Podocarpidites marwickii*, *Trisaccites microsaccatum*; Puerto Visser, Chubut Province, Río Chico Formation, Thanetian (late Paleocene): *Dacrycarpites* cf. *australiensis*, *Dacrydiumites florinii*, *Microcachrydites antarcticus*, *Phyllocladidites mawsonii*, *Podocarpidites marwickii*, *P.* sp. 1; *Brunoa santarosensis*, *Worsdellia bonetiae* (cycads; Late Cretaceous, Río Negro Province, see Artabe et al., 2004)

[13, Tierra del Fuego, core from 14 km south of San Sebastián Bay, Estancia La Sara, Late Cretaceous–Paleocene, all *Nothofagidites* (*Nothofagus* pollen)]

Nothofagidites acromegacanthus (Late Cretaceous (?) to Eocene, principle occurrence Oligocene); *N.* cf. *asperus* (late Paleocene, late Eocene to early Oligocene); *N. cranwellae* [Paleocene (?) to Eocene, Oligocene]; *N. dorotensis* (Cerro Dorotea Formation, Late Cretaceous to early Paleocene, Oligocene); *N. fortispinulosus* (Late Cretaceous, late Eocene to early Oligocene); *N. fuegiensis* [Late Cretaceous (?) to Eocene, Oligocene]; *N. hystricosphaeroides* [Paleocene (?) to Eocene, Oligocene]; *N. kaitangatus* (Cerro Dorotea Formation, Late Cretaceous to early Paleocene, Eocene to Oligocene); *N. paucispinosus* (Late Cretaceous to Eocene, Oligocene); *N. rocaensis* (Jagüel Formation, middle Maastrichtian, Late Cretaceous to Oligocene); *N. saraensis* (Late Cretaceous, Paleocene to Oligocene); *N. suggatei* [Jagüel Formation in Río Negro Province, middle Maastrichtian; Paleocene (?) to Eocene, Oligocene]; *N.* cf. *visserensis* (Late Cretaceous to Eocene, Oligocene); *N.* cf. *waipawensis* (Cerro Dorotea Formation, Late Cretaceous to early Paleocene, Eocene to Oligocene)

Megafossils

[14, Cerro Baguales, Shehuen Valley, Santa Cruz Province, Late Cretaceous (Turonian?)]

Ferns and allied groups: *Dennstaedtia patagonica* (Dennstaedtiaceae), *Dryopterites problematicus*, *Gleichenites piatnitzkyi*. Gymnosperms: *Protophyllocladus australis*. Angiosperms (dicotyledons): *Laurophyllum* (*Nectandra*) *proteaefolium*, *L.* (*Persea*?) *kurtzi*, *Menispermites piatnitzkyi*, *Myrcia santacruzensis* (Myrtaceae), *Paranymphaea proteaefolia*, *Sterculia sehuensis* (Sterculiaceae)

[15, Cuenca Carbonifera de Río Turbio, SSW Santa Cruz, Paleocene (Danian) to early Oligocene; late Eocene to early Oligocene, see Romero, 1986, p. 455; family assignments fide Huniken, 1955; [?] = genera unexpected in the Paleogene of southern South America]

Taxon	**Occurrence**		
	Cerro Dorotea (Danian)	**Río Turbio** (late middle Eocene to early late Eocene)	**Río Guillermo** (early Oligocene)
Ferns			
Polypodiaceae			
Asplenium [Aspleniaceae]		x	
Filicites		x	
Pecopteris sp. 1		x	
Pecopteris sp. 2		x	
Pteris (*Eupteris*?) *frenguellii* [Pteridaceae]		x	
Woodwardia [Blechnaceae]		x	
Sphaen[r]opteridaceae			
Sphaen[*r*]*opteris molinae* [Cyatheaceae]		x	
Gymnosperms			
Araucariaceae			
Araucaria nathorsti			x
A. sp.		x	
Ginkgoaceae			
Ginkgo?			x
Podocarpaceae			
Acmopyle engelhardti [Taxaceae]		x	
Angiosperms			
Dicotyledons			
Anacardiaceae			
Anacardites pichileufensis		x	
A. rioturbioensis	x (?)	x	
Rhoophyllum serratum (fossil)			x
Schinopsis patagonica		x	
Annonaceae			
An(*n*)*ona precochambensis*		x	
A. rioturbioensis		x	
cf. *A. speciosa*		x	
Apocynaceae			
Allamanda crassostipitata		x	
Asclepiadaceae			
Patrisia eocenica		x	
Polioexolobus molinae		x	
Bignoniaceae			
Adenocalymma aff. *tertiaria*		x	
Bignonia gigantifolia		x	
B. pichileufuana		x	

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Taxon	Occurrence		
	Cerro Dorotea (Danian)	**Río Turbio** (late middle Eocene to early late Eocene)	**Río Guillermo** (early Oligocene)
Bignoniaceae (continued)			
Tabebuia ipiformis		x	
Tecoma serrata		x	
Bombacaceae			
Bombax firmifolium		x	
Zizyphus sp. 1		x	
Z. sp. 2		x	
Caesalpiniaceae (Leguminosae)			
Cassia longifolia		x	
Dilleniaceae			
Tetracera rhamnoides		x	
Euphorbiaceae			
Omphalea filiciformis		x	
O. flaviana		x	
Fagaceae			
Dryophyllum australis		x	
Fagaceae undet.	x		
Fagophyllum duseni		x	
Fagus [?] *dicksoni* [*Nothofagus*?]		x	
F. morenoi		x	x
F. obscura		x	x
F. subferruginea	x	x	
Nothofagus australis		x	
N. crenulata			x
N. densi-nervosa		x	
N. elongata		x	x
N. lanceolata		x	x
N. magellanica		x	
N. pulchra		x	
N. serrulata		x	x
N. simplicidens		x	
N. variabilis			
forma *microphylla*	x	x	
forma *oblonga*		x	x
Quercus [?] *angustiloba*		x	
Flacourtiaceae			
Casearia aff. *patagonica*		x	
C. spinuloso-serrata		x	
Guttiferae (Clusiaceae)			
Rheedia cf. *preacuminata*		x	
Hippocrateaceae			
Salacia floribundifolia		x	
Juglandaceae			
Juglans [?] *licciardoensis*		x	
Lauraceae			
Acrodiclidium oligocaenicum		x	
?*Camphoromoea speciosa*		x	
Cinnamomum		x	
Goeppertia		x	
Laurophyllum actinodaphnoides		x	
L. sp. 1		x	
L. sp. 2		x	
Mespilodaphne longifolia		x	
Nectandra chilana		x	
N. prolifica		x	
Notaphoebe neogaea		x	
N. ovatifolia		x	
Oreodaphne piatnitzkyi		x	
Persea microphylla		x	
Phoebe lanceolata		x	
Lecythidaceae—see Myrtaceae			
[Leguminosae—see Caesalpiniaceae, Papilionaceae]			
Magnoliaceae			
Drimys aff. *patagonica*		x	
Malpighiaceae			

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Taxon	Occurrence		
	Cerro Dorotea (Danian)	**Río Turbio** (late middle Eocene to early late Eocene)	**Río Guillermo** (early Oligocene)
Tetrapteris precrebrifolia		x	
Monimiaceae			
cf. *Laurelia guinazui*		x	
L. insularis		x	
Moraceae			
Coussapoa prepliocenica		x	
Myricaceae			
Myrica [?] *premira*		x	
Myristicaceae			
Myristica fossilis		x	
Myrtaceae			
Lecythis (Lecythidaceae)		x	
Myrcia chubutensis		x	
M. reticulato-venosa		x	
Myrtiphyllum bagualense			x
Psidium araciforme		x	
Nymphaeaceae			
Parani[y]mphaea? patagonica		x	
Papilionaceae (Leguminosae)			
?*Stenolobium rhomboidalis*		x	
Piperaceae			
Arthante geniculatoides		x	
Platanaceae			
Platanus [?] *patagonica*		x	
Proteaceae			
Lomatia cf. *serrulata*		x	
Rhamnaceae			
Rhamnus fortinervosus		x	
R. sanctaeflaviaensis		x	
R. sp.		x	
Rutaceae			
Erythrochy[i]ton borrelloensis		x	
Sapindaceae			
Allophylus graciliformis		x	
Cupania grosse-serrata		x	
C. latifolioides		x	
C. patagonica		x	
C. aff. *vernaliformis*		x	
C. sp.		x	
Matayba marginatifolia	x	x	
Sapotaceae			
Chrysophyllum		x	
Pouterlabatia clarki		x	
P. lanceolata		x	
Saxifragaceae			
Escallonia frenguellii		x	
Hi[y]drangea? incerta		x	
Sterculiaceae			
Bue(y)ttneria asterotrichiformis		x	
B. lanceolatifolia		x	
Guazuma		x	
Sterculia guinazui		x	
S. washburnii		x	
Styracaceae			
Styrax coriacea		x	
S. glabratoides		x	
S. *glandulifera*		x	
Tiliaceae			
Triumph[f]etta irregulariter-serrata		x	
Ulmaceae			
Momisia		x	

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Microfossils

[16, Río Turbio, SW Santa Cruz Province, Cerro Dorotea Formation, Maastrichtian to Danian, under K in Appendices 2.1, 2.2]

Ferns and allied groups: *Laevigatosporites ovatus*, *Leiotriletes*. Gymnosperms: *Dacrydiumites* (Podocarpaceae, *Dacrydium*; Petriella & Archangelsky, 1975) *florinii*, *Monosulcites* cf. *granulatus*, *M. pseudospinosus*, *Podocarpidites marwickii*, *Trisaccites microsaccatus*. Angiosperms: *Anacolosidites*, *Liliacidites crassibaculatus*, *L. variegatus*, *Myrtaceidites* cf. *mesonesus*, *Psilatricolpites patagonicus*, *P. pulcherrimum*, *Rhoipites*, *Tricolpites retielegans*, *T.* sp., *Tricolporites*, *Triorites* cf. *minor*, *T. minusculus*

[17, Paso del Sapo, Chubut Province, Paso del Sapo Formation, Late Cretaceous]

Ferns and allied groups: *Azolla* (Salviniaceae), *Clavifera triplex*, *Conbaculatisporites*, *Converrucosisporites*, *Deltoidospora minor*, *Dictyophyllidites* (Dipteridaceae; Petriella & Archangelsky, 1975) *mortoni*, *Gleicheniidites senonicus*, *Granulatisporites*, *Hamulatisporis*, *Ischyosporites*, *Klukisporites pachydictyus*, *Laevigatosporites* cf. *discordatus*, *L. gracilis*, *L. ovatus*, *L. vulgaris*, *Leptolepidites*, *Lycopodiumsporites*, *Marattisporites scabratus*, *Neoraistrickia*, *Polypodiidites*, *Stereisporites antiquasporites*, *Todisporites major*, *Waltzispora*

[18, Neuquén Province, Allen (late Campanian–Maastrichtian) and Jagüel (Maastrichtian) formations]

Ferns and allied groups: *Grapnelispora evansii*

[19, Colorado Basin, Buenos Aires Province, Pedro Luro Formation; formation?, Maastrichtian–Paleocene, palynomorphs Danian; under K in Appendices 2.1, 2.2; affinities suggested by the author are cited when given to a specific family]

Ferns and allied groups: *Achradosporis lurensis*, *Azolla* (Salviniaceae), *Biretisporites* (Osmundaceae), *Deltoidospora australis*, *D. minor*, *D. neddeni*, *Dictyophyllidites mortoni*, *Gleicheniidites senonicus* (Gleicheniaceae), *Interulobites variabilis*, *Retitriletes austroclavatidites* (Lycopodiaceae), *Todisporites* cf. *minor* (Osmundaceae). Gymnosperms: *Callialasporites trilobatus* (Araucariaceae), *Classopollis classoides*, *Ephedripites* (Ephedraceae/Araceae) [possibly Araceae], *Gamerroites psilasaccus* (Podocarpaceae), *Microcachryidites antarcticus* (Podocarpaceae), *Podocarpidites marwickii* (Podocarpaceae), *P. rugulosus*, *P. verrucosus*. Angiosperms (monocotyledons): *Liliacidites variegatus*, *Monosulcites minutiscabratus* (Palmae). Angiosperms (dicotyledons): *Ailanthipites*, *Anacolosidites diffusa* (Olacaceae), Chenopodiaceae–Amaranthaceae [in Cretaceous–Danian?], *Myrtaceidites mesonesus* (Myrtaceae), *Proteacidites parvus* (Proteaceae), *P. subscabratus*, *Psilatricolpites patagonicus*, *Psilatricolporites* cf. *salamanquensis*, *Retitricolporites chubutensis* (Anacardiaceae[?]), *Rhoipites baculatus*, *R. minusculus*, *Rosannia manika*, *Srivastapollenites exoticus* (?Loranthaceae), *Striatricolporites gamerroi*, *Triatriopollenites bertelsii*, *T. lateflexus*, *Tricolpites gillii* (Proteaceae), *T. reticulata* (Haloragaceae), *Verrustephanoporites simplex* (Ulmaceae, *Phyllostylon*[?]). Incertae sedis: *Catinipollis geiseltalensis*, *Mtchellishvilia saltenia*

[20, Arroyo Agua del Choique, Mendoza Province, Malargüe Formation, Late Cretaceous]

Algae: *Botryococcus*, *Pediastrum*. Ferns and allied groups: *Azolla* (Salviniaceae), *Deltoidospora australis*, *D. minor*, *Gleicheniidites* (Gleicheniaceae), *Grapnelispora*, *Laevigatosporites ovatus*, *Pustulatisporites*. Gymnosperms: *Alisporites australis*, *Araucariacites australis* (Araucariaceae), *Callialasporites trilobatus* (Araucariaceae), *Classopollis*, *Cycadopites granulatus* (Cycadales), *Equisetosporites minuticostatus*, *Microcachryidites*, *Phrixipollenites*. Angiosperms (monocotyledons): *Liliacidites*. Angiosperms (dicotyledons): *Peninsulapollis gillii* (Magnoliaceae?), *Psilatricolpites*, *Psilatricolporites*, *Rhoipites*, *Triporopollenites lateflexus*

Paleocene

Megafossils

[21, Telsen–Rosada region, Chubut Province, La Colonia Formation, Maastrichtian]

Ferns and allied groups: *Paleoazolla patagonica* (Salviniaceae)

[22, Cerro Abigarrado, Chubut Province, Salamanca Formation, Paleocene (Danian)]

Angiosperms (monocotyledons): *Palmoxylon patagonium* (Palmae)

[23, Los Menucos, Río Negro Province, formation?, Early Tertiary(?)]

Gymnosperms: *Menucoa cazaui* (Cycadales)

[24, Las Plumas, Chubut Province, Cerro Bororó Formation, Paleocene]

Gymnosperms: *Bororoa andreisii*, *B. anzulovichii* (Cycadales), *Mesembrioxylon mazzonii* (Podocarpaceae, or possibly angiospermous fide original author p. 159). Angiosperm (monocotyledon): *Palmoxylon*. Angiosperms (dicotyledons): *Brideliоxylon americanum* (Euphorbiaceae), *Elaeocarpoxylon sloanoides* (Elaeocarpaceae), *Euxylophoroxylon chiquichanensis* (Rutaceae), *Rhizophoroxylon spallettii* (Rhizophoraceae), *Weinmannioxylon multiperforatum*, *W. pluriradiatum* (Cunoniaceae). Incertae sedis: *Dryoxylon*

[25, 26, 27, Laguna del Hunco, near Cerro Mirador, Chubut Province, Laguna del Hunco Series, radiometric date of 57 ± 3 Ma (Paleocene, Thanetian; Archangelsky, 1974)]

25—Angiosperms (dicotyledons): *Akania americana* (Akaniaceae); 26—*Lomatia bivascularis* (Proteaceae); 27—*Roupala patagonica* (Proteaceae); Romero, 1986: *Annona* (Annonaceae), *Casuarina* (Casuarinaceae), *Cochlospermum* (Cochlospermaceae), *Peumus* (Monimiaceae), *Schniopsis* (Anacardiaceae)

[28, Cerro Funes, margin of Pampa Maria Santisima, Chubut–Santa Cruz provinces, Río Chico Formation, Paleocene]

Angiosperms (dicotyledons): *Banaraphyllum ovatum* (Flacourtiaceae), *Cissites patagonica* (Vitaceae), *Cryptocaryoides maria-santisimenis* (Lauraceae), *Dryophyllum australis* (Fagaceae), *Fagophyllum duseni* (Fagaceae), *Laurophyllum* (*Nectandra*) *chubutensis*, *L.* (*Oreodaphne*) *piatnitzkyi* (Lauraceae), *Myrica premira* (Myricaceae), *Paranymphaea aristolochiaformis* (Nymphaeaceae), *Sterculia acuminataloba* (Sterculiaceae), *Zizyphus chubutensis* (Rhamnaceae)

Microfossils

[29, Cerro Abigarrado, Puerto Visser, Bajada de Hansen (Salamanca Formation), Bororó Formation, subsurface cores, Chubut Province, Paleocene]

Ferns and allied groups: *Baculatisporites turbioensis*, *Biretisporites*, *Cingutriletes australis*, *Clavifera triplex* (Gleicheniaceae; Petriella & Archangelsky, 1975), *Cyatheacidites* cf. *annulata*(*us*), *Cyathidites minor*, *C. patagonicus*, *Dictyophyllidites concavus*, *Gleicheniidites senonicus*, *Laevigatosporites ovatus*, *Leiotriletes regularis*, *Lycopodiumsporites austroclavatidites*, *Matonisporites*, *Neoraistrickia*, *Trilites paravallatus*, *Tuberculatosporites parvus*. Gymnosperm: *Cycadopites*. Angiosperms (monocotyledons): *Confertisulcites* (Palmae; Petriella & Archangelsky, 1975), *Liliacidites regularis*, *L. variegatus*, *Longapertites andreisii*, *L. patagonicus*, *Monosulcites minutiscabratus* (Palmae; Petriella & Archangelsky, 1975), *Pandaniidites* (Pandanaceae), *Proxaperites operculatus* (Palmae; Petriella & Archangelsky, 1975), *Restioniidites pascualii* (Restionaceae; Petriella & Archangelsky, 1975), *Sabalpollenites* (Palmae; Petriella & Archangelsky, 1975), *Sparganiaceaepollenites*, *Spinozonocolpites* (Palmae, *Nypa*). Angiosperms (dicotyledons): *Albertipollenites angululuminosus*, *Anacolosidites diffusa* (Olacaceae), *Favitricolporites australis*, *Gemmatricolpites subsphaericus*, *Haloragacidites harrisii*, *Polyporina romeroi*, *Proteacidites*, *Psilatricolpites inargutus*, *P. psilascabratus*, *Psilatricolporites*, *Retidiporites camachoi* (Proteaceae; Petriella & Archangelsky, 1975), *Retitricolporites chubutensis*, *Rhoipites* (Cunoniaceae; Petriella & Archangelsky, 1975) *baculatus*, *R. minusculus*, *Rousea patagonica*, *Senipites tercrassata* (Symplocaceae, *Symplocus*?), *Striatricolporites gamerroi*, *Syndemicolpites petriellai* (Loranthaceae), *Triatriopollenites bertelsii* (Myricaceae?), *T. lateflexus* (Proteaceae), *Tricolpites communis*, *"T." gillii*, *T.* cf. *reticulata* (Haloragidaceae), *Ulmoideipites patagonicus* (Ulmaceae)

[30, Chubut Province, various sites–core samples, Salamanca and Bororó formations, Paleocene]

Angiosperms (monocotyledons): *Liliacidites regularis*, *L. vermireticulatus*, *Spinozonocolpites hialinus*. Angiosperms (dicotyledons): *Callistopollenites*, *Ericipites*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

microtectatum (Empetraceae), *E. scabratus*, *Psilatricolporites salamanquensis*, *Retitricolporites chubutensis*, *Rousea microreticulata*, *R. minuscula*, *Striatopollis exiguus*, *Tricolpites bibaculatus*. Incertae sedis: *Catinipollis geiseltalensis*

[31, 32, Salta Province, Salta Group, Tunal Formation, Paleocene]

Fungi: *Dicellaesporites*, *Multicellaesporites*. Algae: *Pediastrum*. Gymnosperm: *Podocarpidites marwickii* (Podocarpaceae). Angiosperms (dicotyledons): *Ailanthipites*, *Clavatricolpites* cf. *gracilis*, *Ephedripites* (gymnosperm, Ephedraceae; angiosperm, Araceae), *Gemmatricolpites subsphaericus* (Aquifoliaceae), *Myriophyllumpollenites* (Haloragaceae), *Pandaniidites texus* (Pandanaceae), *Retitricolporites* sp. A (Anacardiaceae), *Rhoipites* (Anacardiaceae) cf. *minusculus*, *Verrustephanoporites* cf. *simplex* (Ulmaceae, *Phyllostylon*). Incertae sedis: *Mtchedlishvilia saltenia*

[33, Salta Basin, Alemania subbasin, Salta, NW Argentina, Maíz Gordo Formation, Paleocene]

Ferns and allied groups (incertae sedis): *Dictyophyllidites* (Dipteridaceae), *Espora apiculada*. Gymnosperm: *Podocarpidites marwickii*. Angiosperms (dicotyledons): *Corsinipollenites menendezii* (Onagraceae), *Cricotriporites* cf. *guianensis*, *Echistephanoporites* cf. *alfonsi*, *Retitricolporites medius*, *Rhoipites* cf. *minusculus*, *Rousea* cf. *patagonica*, *Tricolpites* cf. *reticulata* (Gunneraceae), *Triorites*, *Verrustephanoporites* cf. *simplex*

[34, 35, Pampa Grande, Salta Province, Salta Group, Lumbrera Formation, late Paleocene to early Eocene; see also del Papa et al., 2002]

Fungi: *Dicellaesporites*, *Diporisporites elongatus*, *Inapertisporites ovalis*, *Pluricellaesporites*. Ferns and allied groups: *Baculatisporites*, *Gabonisporis vigourouxii* (Marsileaceae), *Laevigatosporites*, *Retitriletes austroclavatidites* (*Lycopodium*). Gymnosperms: *Inaperturopollenites* (Araucariaceae), *Podocarpidites* cf. *marwickii*. Angiosperm (monocotyledon): *Smilacipites saltensis* (Liliaceae, *Smilax*). Angiosperms (dicotyledons): *Jussitriporites menendezii* (Onagraceae), *Liquidambarpollenites* cf. *brandonensis* (Hamamelidaceae [?], *Liquidambar* [?]), *Nothopollenites* (Combretaceae), *Rhoipites* sp. A (Rutaceae, *Ruta*), *Tricolpites* (*Psilatricolpites*) *lumbrerensis*, *T.* cf. *reticulatus*, *T. vulgaris* (Hamamelidaceae), *Verrustephanoporites simplex*

[36, Cuenca del Colorado, Buenos Aires Province, Salta Group, Pedro Luro Formation, late Danian, Paleocene]

Angiosperm (dicotyledon): *Srivastavapollenites exoticus* (Loranthaceae?)

[37, Garabatal Creek, Jujuy Province, Salta Group, Mealla Formation, middle to late Paleocene]

Algae: *Catinipollis geiseltalensis* (Zygnemataceae or incertae sedis). Ferns and allied groups: *Apiculatisporis*, *Azolla* (Salviniaceae), *Baculatisporites*, *Biretisporites* (Osmundaceae), *Deltoidospora*, *Grapnelispora evansii*, *Ischyosporites* (Schizaeaceae). Angiosperms (monocotyledons): *Liliacipites variegatus*, *Spinozonocolpites* (Palmae, *Nypa*). Angiosperms (dicotyledons): *Ailanthipites* (Anacardiaceae), *Clavatricolpites* cf. *gracilis*, *Corsinipollenites menendezii* (Onagraceae), *Ephedripites* (Araceae), *Gemmatricolpites subsphaericus* (Aquifoliaceae), *Liquidambarpollenites* cf. *brandonensis* (Hamamelidaceae [?], *Liquidambar* [?]), *Myriophyllumpollenites* (Haloragaceae), *Pandaniidites texus* (Pandanaceae), *Psilatricolpites acerbus*, *P. simplex*, *Restioniidites* (Restionaceae), *Retitricolporites chubutensis*, *Rhoipites baculatus* (Mimosaceae), *R. minusculus* (Loganiaceae), ?*R.* sp. A (Rutaceae), *Rousea patagonica*, *Tricolpites bibaculatus* (?Flacourtiaceae), *T. communis*, *T.* cf. *reticulata* (Gunneraceae), *Verrustephanoporites simplex* (Ulmaceae, *Phyllostylon*). Incertae sedis: *Catinipollis geiseltalensis*

Eocene

Megafossils

[38, Río Turbio, Santa Cruz Province, Río Turbio Formation, Eocene (probably early Eocene fide Romero & Zamaloa, 1985)]

Angiosperms (monocotyledon): *Poacites* (Gramineae). Angiosperms (dicotyledons): *Berberis boweri* (Berberidaceae), *Embothriophyllum dubium* (Proteaceae), *Fagus dicksoni*, *F. integrifolia*, *F. subferruginea* (Fagaceae [generic identification?, *Nothofagus*?]), *Nothofagus elongata*, *N. variabilis* (Fagaceae), *Rhoophyllum serratum* (Anacardiaceae)

[39, Bahia Solano, east of Pico Salamanca, Chubut Province, Patagonica Formation (?), Eocene]

Angiosperm (dicotyledon): *Ulminium atlanticum* (Lauraceae)

[40, Bariloche, Río Negro Province, Ñirihuau Formation, Eocene]

Angiosperms (dicotyledons): *Myrcia deltoidea* (Myrtaceae). Incertae sedis: *Phyllites*

[41, Río Pichileufu, NW Patagonia, Ventana Formation, early Eocene (Romero, 1986, p. 454); early Miocene (Berry, 1938); current studies Laguna del Hunco, Wilf et al., 2005)]

Ferns and allied groups: *Asplenium incertum*, *Dicksonia patagonica* (Cyatheaceae), *Goniopteris patagoniana* (Polypodiaceae). Gymnosperms: *Araucaria pichileufensis* (Araucariaceae), *Fitzroya tertiaria* (Cupressaceae), *Ginkgo patagonica* (Ginkgoaceae), *Libocedrus prechilensis* (Cupressaceae), *Podocarpus andiniformis*, *P. engelhardti* (Podocarpaceae), *Zamia tertiaria* (Cycadaceae). Angiosperms (monocotyledon): *Poacites chloriformis* (Gramineae). Angiosperms (dicotyledons): *Acrodiclidium oligocaenicum* (Lauraceae), *Adenocalymma tertiaria* (Bignoniaceae), *Allemanda crassostipitata* (Apocynaceae), *Allophylus eduliformis*, *A. graciliformis* (Sapindaceae), *Ampelodaphne grandifolia* (Lauraceae), *Anacardites brittoni*, *A. pichileufensis* (Anacardiaceae), *Annona infestans* (Annonaceae), *Ardisia crassifolia* (Myrsinaceae), *Astronium argentinum* (Anacardiaceae), *Azara celastriniforma*, *A. tertiaria* (Flacourtiaceae), *Banara cuadrae*, *B. prehernandiensis* (Flacourtiaceae), *Banisteria patagonica* (Malpighiaceae), *Berberis corymbosifolia* (Berberidaceae), *Bignonia pichileufuana* (Bignoniaceae), *Bue(y)ttneria asterotrichiformis*, *B. lanceolatifolia* (Sterculiaceae), *Bumelia australis* (Sapotaceae), *Casearia patagonica* (Flacourtiaceae), *Cassia argentinensis*, *C. longifolia*, *C. oxleyi*, *C. patagonica* (Leguminosae), *Cedrela mexicaniformis*, *C. pichileufuana* (Meliaceae), *Celastrophyllum elaeodendriforme*, *C. fraunhoferifolium* (Celastraceae), *Celtis ameghinoi* (Ulmaceae), *Cephalanthus glabratifolius* (Rubiaceae), *Cissus pichileufensis* (Vitaceae), *Coccoloba ruizianiforma* (Polygonaceae), *Cochlospermum previtifolium* (Cochlospermaceae), *Coprosma incerta*, *C. spathulatifolia* (Rubiaceae), *Coussarea tertiaria* (Rubiaceae), *Cupania cordinii*, *C. grosse-serrata*, *C. latifolioides*, *C. patagonica*, *C. vernaliformis* (Sapindaceae), *Dalbergia patagonica* (Leguminosae), *Diatenopteryx fossilis*, *D. sorbifoliiforma* (Sapindaceae), *Drimys patagonica* (Winteraceae), *Echites tertiaria* (Apocynaceae), *Embothrium precoccineum*, *E. pregrandiflorum* (Proteaceae), *Erythroxylon cuneifolioides* (Erythroxlaceae), *Eucryphia tertiaria* (Eucryphiaceae), *Fagara serrata* (Rutaceae), *Ficus patagonica* (Moraceae), *Goeppertia ovalifolia* (Lauraceae), *Hoffmannia protogaea* (Rubiaceae), *Hydrangea*? *incerta* (Saxifragaceae), *Icica pichileufuana* (Burseraceae), *Inga patagonica* (Leguminosae), *Landolphia paraparaensis* (Apocynaceae), *Laurelia guiñazui* (Monimiaceae), *Leptolobium prenitens* (Leguminosae), *Lomatia preferruginea* (Proteaceae), *Malvacarpus guinazui* (Malvaceae), *Mascagnia sepiumoides* (Malpighiaceae), *Matayba marginatifolia* (Sapindaceae), *Maytenus ellipticus*, *M. latifolioides* (Celastraceae), *Momisia australis* (Ulmaceae), *Myrceugenia tertiaria*, *Myrcia chubutensis*, *M. deltoidea*, *M. obovata*, *M. reticulato-venosa* (Myrtaceae), *Myrica mira* (Myricaceae), *Myristica*? *fossilis* (Myristicaceae), *Nectandra patagonica*, *N. prolifica* (Lauraceae), *Notaphoebe neogaea*, *N. ovatifolia* (Lauraceae), *Nyctaginites ellipticus* (Nyctaginaceae), *Omphalea patagonica* (Euphorbiaceae), *Oreodaphne preacutifolia* (Lauraceae), *Oreopanax guinazui* (Araliaceae), *Ouratea firmifolia* (Ochnaceae), *Paullinia prerufescens*, *P. rubiginosifolia* (Sapindaceae), *Phoebe elliptica*, *P. lanceolata* (Lauraceae), *Plumiera articulatifolia* (Apocynaceae), *Polioexolobus prenuntius* (Asclepiadaceae), *Polylepis prenuntia* (Rosaceae), *Pouterlabatia clarki*, *P. lanceolata* (Sapotaceae), *Psidium araciforme* (Myrtaceae), *Remijia tenuiflorifolia* (Rubiaceae), *Rondeletia longiflorifolia* (Rubiaceae), *Rubiacites chomeliifolia* (Rubiaceae), *Salacia floribundifolia* (Hippocrateaceae), *Sapindus argentinus* (Sapindaceae), *Schinopsis balansiformis*, *S. morongifolia*, *Schinus molliformis* (Anacardiaceae), *Sterculia guinazui*, *S. patagonica*, *S. washburnii* (Sterculiaceae), *Strychnos patagonica* (Loganiaceae), *Styloceras tertiarium* (Buxaceae), *Styrax acuminatiformis*, *S. glandulifera* (Styracaceae), *Symplocos commutatifolia* (Symplocaceae), *Tabebuia ipiformis* (Bignoniaceae), *Tetracera patagonica* (Dilleniaceae), *Tetrapteris precrebrifolia* (Malpighiaceae), *Trichilia catignoides*, *T. moritziformis* (Meliaceae), *Triumfetta irregulariter-serrata* (Tiliaceae), *Villaresia congonhifolia* (Icacinaceae). Incertae sedis: *Carpolithus patagonicus*, *C. pichileufensis*, *Phyllites*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Microfossils

[42, Río Turbio, Santa Cruz Province, Río Turbio Formation, middle Eocene]

Ferns and allied groups: *Baculatisporites comaumensis*, *B. turbioensis*, *Biretisporites crassilabratus*, *Cingutriletes australis*, *Concavisporites*, *Corrugatisporites argentinus*, *Cyatheacidites annulatus*, *Cyathidites minor*, *C. patagonicus*, *Deltoidospora*, *Gleicheniidites senonicus*, *Laevigatosporites ovatus*, *Leiotriletes regularis*, *Leptolepidites densus*, *Lycopodiumsporites austroclavatidites*, *L.* cf. *eminulus*, *Peromonolites*, *Polypodiidites speciosus*, *Reticuloidosporites* cf. *tenellis*, *Trilites fasolae*, *T. parvallatus*, *Tuberculatosporites parvus*

[43, Río Turbio coal mine area, Santa Cruz Province, Río Turbio Formation, middle Eocene]

Gymnosperms: *Araucariacites australis* (Araucariaceae), *Dacrycarpites australiensis* (Podocarpaceae), *Dacrydiumites florinii* (Podocarpaceae), *Equisetosporites notensis* (Ephedraceae), *Microcachrydites antarcticus* (Podocarpaceae), *Phyllocladidites mawsonii*, *P. ruei* (Podocarpaceae), *Podocarpidites elegans*, *P. magnus*, *P. marwickii*, *P. microreticuloidata*, *P. rugulosus* (Podocarpaceae), *Trisaccites microsaccatum*. Angiosperms (dicotyledons, all Fagaceae, *Nothofagidites*): *Nothofagidites asperus*, *N. brachispinulosa*, *N. cincta*, *N. cranwellae*, *N. deminuta*, *N. fortispinulosus*, *N. micromarginata*, *N. nana*, *N. saraensis*

[44, SW Santa Cruz Province, Río Turbio Formation, Eocene]

Angiosperms (dicotyledons): *Bysmapollis verrucosus*, *Ericipites*, *Intratriporopollenites*, *Myrtaceidites verrucosus*, *Periporopollenites demarcatus*, *Tricolpites angululuminosus*, *T. incisus*, *T. reticulatus*

[45, SW Santa Cruz Province, Río Turbio Formation, Eocene]

Fungi: *Dyadosporonites annulatus*, *Lacrimasporonites*, *Plochmopeltinites masonii* (Microthyriaceae), *Pluricellaesporites psilatus*. Angiosperms (dicotyledons): *Concolpites leptos*, *Gothanipollis bassensis* (Loranthaceae), *Ilexpollenites clifdenensis* (*Ilex*, Aquifoliaceae), *Striatricolporites gamerroi*, *Triatriopollenites lateflexus* (Myricaceae), *Tricolpites gillii* (Proteaceae), *T. reticulatus*[*a*] (Gunneraceae)

[46, Bahia Sloggett, Tierra del Fuego, Sloggett Formation, late Eocene]

Algae: *Botryococcus braw(u)nii*. Ferns and allied groups: *Baculatisporites comaumensis*, *B. turbioensis*, *Biretisporites crassilabratus*, *Cingutriletes australis*, *Corrugatisporites argentinus*, *Cyatheacidites annulatus*, *Cyathidites minor*, *Foveotriletes palaequetrus*, *Laevigatosporites ovatus*, *Lycopodiumsporites austroclavatidites*, *Muricingulisporis chenquensis*, *Peromonolites vellosus*, *Polypodiisporites*, *Trilites parvallatus*. Gymnosperms: *Araucariacites australis*, *Gamerroites psilasaccus*, *Lygistepollenites florinii*, *Phylocladidites mawsonii*, *P.* cf. *verrucosus*, *Podocarpidites elegans*, *P. ellipticus*, *P.* cf. *exiguus*, *P. rugulosus*, *Trisaccites microsaccatum*. Angiosperms (dicotyledons): *Myrtaceidites verrucosus*, *Nothofagidites acromegacanthus*, *N. dorotensis*, *N. saraensis*, *N. tehuelchesii* [Fagaceae], *Proteacidites*, *Pseudowinterapollis couperi*, *Rhoipites*, *Tricolpites reticulatus*, *Triorites minor*

[47, NE Tierra del Fuego, Cullen Formation, Miocene; Zamaloa, 2000]

Algae: *Catinipollis geiseltalensis* (Zygnemataceae), Zamaloa (1996) adds Zygnemataceae–*Mougeotia* cf. *laetivirens*, *M.* sp., *Spirogyra* (3 types), *Zygnema* (2 types). Bryophyta: *Reboulisporites fuegiensis* (Rebouliaceae). Ferns and allied groups: *Baculatisporites comaumensis* (Osmundaceae), *Lycopodiumsporites eminulus* (Lycopodiaceae, *Lycopodium*). Gymnosperm: *Phyllocladidites mawsonii* (Podocarpaceae, *Dacrydium*). Angiosperms (dicotyledons): *Crassiorites australis* (Onagraceae; *Fuchsia* type), *Malvacipollis argentina* (Malvaceae), *Nothofagidites suggatei* (Fagaceae, *Nothofagus*)

[48, Arroyo Chenqueniyeu, Río Negro Province, Ventana Formation?, Oligo–Miocene (early Eocene, see Romero, 1986, p. 454)]

Angiosperm (dicotyledon): *Ruprechtia latipedunculata* (Polygonaceae)

[49, Aries x-1 Well, continental shelf, offshore Tierra del Fuego, formation?, Oligo–Miocene; fungal spore(s) present but not named; dinoflagellates not included here]

Algae: *Botrycoccus braw(u)nii*, *Pediastrum* sp., zygospores of Zygnemataceae. Ferns and allied groups: *Baculatisporites*, *Cingutriletes australis*, *Cyatheacidites annulatus*, *Cyathidites minor*, *Foveotriletes palaequetrus*, *Gleicheniidites*, *Ischyosporites areapunctatis*, *Laevigatosporites ovatus*, *Matonisporites ornamentalis*, *Monolites alveolatus*, *Peromonolites radiatus*, *P. vellosus*, *Retitriletes austroclavatidites*, *Rouseisporites*. Gymnosperms: *Araucariacites australis*, *Assamiapollenites incognitus*, *Equisetosporites claricristatus*, *E. notensis*, *Gamerroites* cf. *psilasaccus*, *Lygistepollenites florinii*, *Microcachryidites antarcticus*, *Phyllocladidites mawsonii*, *Podocarpidites elegans*, *P.* cf. *ellipticus*, *P. marwickii*, *P. rugulosus*, *Trisaccites microsaccatum*. Angiosperms: *Arecipites subverrucatus*, *Baumannipollis variaperturatus*, *Chenopodipollis chenopodiaceoides*, *Clavatipollenites*, *Corsinipollenites atlantica* [Onagraceae], *Cupanieidites reticularis*, *Cyperaceaepollis neogenicus* (Cyperaceae), *Diporites*, *Ericipites*, *Graminidites* [Gramineae], *Liliacidites*, *Margocolporites tenuireticulatus*, *Multisiapollis viteauensis*, *Myrtaceidites verrucosus*, *Nothofagidites acromegacanthus*, *N. americanus*, *N. dorotensis*, *N. flemingii*, *N. saraensis*, *N. tehuelchesii* [Fagaceae], *Poluspissusites*, *Proteacidites pseudomoides*, *Pseudowinterapollis couperi*, *Psilatricolporites operculatus* [Euphorbiaceae, *Alchornea*], *Rhoipites baculatus*, *R. cienaguensis*, *Sparcipollis*, *Sparganiaceaepollenites barungensis* (Sparganiaceae), *Striasyncolpites laxus*, *Striatricolporites gamerroi*, *Tricolpites reticulatus*, *T. trioblatus*, *Triporopollenites*

[50, Precordillera Central, San Juan Province, Pachaco Formation, late Eocene to Miocene]

Algae: *Pediastrum* cf. *duplex*. Ferns and allied groups: *Divisisporites*, *Polypodiidites inangahuensis*, *Todisporites major* (Osmundaceae). Gymnosperms: *Dacrydiumites florinii* (Podocarpaceae, *Dacrydium*), *Ephedripites multipartitus* (*Ephedra*), *Microcachryidites antarcticus* (Podocarpaceae, *Microcachrys*), *Podocarpidites marwickii*, *P.* cf. *verrucosus* (Podocarpaceae), *Protodiploxypinus*. Angiosperms (monocotyledons): *Potamogetonaceaepites* (Potamogetonaceae, *Potamogeton*, cf. *P. pectinatus*), *Smilacipites saltensis* (*Smilax*), *Sparganiaceapollenites* cf. *barungensis* (Sparganiaceae, *Sparganium*). Angiosperms (dicotyledons): *Ailanthipites* cf. *marginatus* (Anacardiaceae [?]), *Margocolporites* (Bignoniaceae, *Jacaranda*), *Myrtaceidites* (Myrtaceae), *Nothofagidites* cf. *incrassatus* (Fagaceae, *Nothofagus*), *N. micromarginatus*, *N. saraensis*, *N. visserensis* (Fagaceae), *Polyporina romeroi*, *Psilatricolpites psilascabratus*, *Psilatricolporites*, *Rhoipites* cf. *baculatus* (Rutaceae, *Ruta*), *Tricolpites reticulatus* (Gunneraceae, "probably *Gunnera*")

[51, Playa La Mina, Santa Cruz Province, San Julián Formation, late Oligocene]

Bryophyta: *Cingutriletes australis* (*Sphagnum*). Ferns and allied groups: *Baculatisporites turbioensis*, *Biretisporites crassilabratus*, *Cyatheacidites annulatus* (Lophosoriaceae, *Lophosoria quadripinnata*), *Cyathidites paleospora* (Cyatheaceae, *Cyathea*), *Deltoidospora*, *Ischyosporites areapunctatis* (Schizaeaceae?), *Laevigatosporites ovatus* (Blechnaceae [and other families—Pteridaceae, Polypodiaceae]), *Lycopodiumsporites austroclavatidites* (Lycopodiaceae, *Lycopodium*), *Matonisporites ornamentalis*, *Muricingulisporis chenquensis* (Pteridaceae, *Pteris semiadnata*), *Peromonolites vellosus* (Athyriaceae [Dryopteridaceae]), *Polypodiisporites inangahuensis*, *P. radiatus* (Polypodiaceae [and other families]), *Reticuloidosporites tenellis*. Gymnosperms: *Araucariacites australis* (Araucariaceae), *Equisetosporites claricristatus* (Ephedraceae), *Gamerroites* cf. *psilasaccus* (Podocarpaceae), *Lygistepollenites florinii* (Podocarpaceae), *Microcachryidites antarcticus* (Podocarpaceae, *Microcachrys tetragona*), *Phyllocladidites mawsonii* (Podocarpaceae, *Dacrydium franklinii*), *P.* cf. *verrucosus* (Podocarpaceae), *Podocarpidites elegans*, *P. marwickii* (Podocarpaceae), *Trisaccites microsaccatum* (Podocarpaceae). Angiosperms (monocotyledons): *Arecipites* cf. *minutiscabratus* (Palmae), *Graminidites* (Gramineae), *Liliacidites variegatus* (Palmae), *Sparganiaceaepollenites barungensis* (Sparganiaceae, *Sparganium*). Angiosperms (dicotyledons): *Baumannipollis variaperturatus* (Malvaceae), *Bredeliapollis* (Combretaceae, *Combretum–Terminalia*), *Canthiumidites* aff. *bellus* (Rubiaceae, *Gardenia* [? presently Paleotropical]), *Chenopodipollis* (Chenopodiaceae [chenoam]), *Clavatipollenites* (Chloranthaceae), *Compositoipollenites* aff. *tarragoensis* (Compositae; oldest record of Compositae for Patagonia, Viviana Barreda, pers. comm., 2003; also listed but not illustrated, *Tubulifloridites*), *Cupanieidites reticularis* (Sapindaceae, *Cupania*), *Diporites aspis* (Onagraceae, *Fuchsia*), *Margocolporites tenuireticulatus*, *Myrtaceidites verrucosus* (Myrtaceae), *Nothofagidites acromegacanthus*, *N. americanus*, *N. dorotensis*,

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

N. flemingii, *N. saraensis*, *N. tehuelchesii* (Fagaceae, *Nothofagus*), *Nyssapollenites endobalteus* (Euphorbiaceae), *Poluspissusites* (Goodeniaceae), *Proteacidites obscurus* (Proteaceae), *Pseudowinterapollis couperi* (Winteraceae, [*Drimys*?]), *Rhoipites baculatus*, *Senipites patagonica* (Symplocaceae, *Symplocos*), *Sparcipollis*, *Spinitricolpites*, *Striatricolporites gamerroi* (Anacardiaceae), *Tricolpites asperamarginis* (Violaceae?), *T. reticulatus* (Gunneraceae, *Gunnera*), *Tubulifloridites* (Compositae)

[52, Gulf of San Jorge, Chubut and Santa Cruz provinces, Chenque Formation, early Miocene (Palamarczuk & Barreda, 1998; Barreda & Palamarczuk, 2000b); for suggested affinities of several of the angiosperms see Ref. 51 above; under Oligocene, Oligo–Miocene in Appendices 2.1, 2.2]

Algae: *Botryococcus braunii*, *Pediastrum*, *Tasmanites*. Bryophyta: *Cingutriletes australis*. Ferns and allied groups: *Azolla*, *Baculatisporites turbioensis*, *Biretisporites crassilabratus*, *Cyatheacidites annulatus*, *Cyathidites minor*, *C. paleospora*, *C. patagonicus*, *Deltoidospora*, *Faveasporis areapunctatis*, *F. palaequetrus*, *Foveotriletes palaequetrus*, *Gleicheniidites circinidites*, *Ischyosporites areapunctatis*, *Laevigatosporites ovatus*, *Leiotriletes* cf. *regularis*, *Lycopodiumsporites austroclavatidites*, *Matonisporites ornamentalis*, *Muricingulisporis chenquensis*, *Peromonolites vellosus*, *Polypodiisporites inangahuensis*, *P.* cf. *minimus*, *P. radiatus*, *Reticuloidosporites tenellis*, *Todisporites*, *Trilites paravallatus*. Gymnosperms: *Araucariacites australis*, *Dacrycarpites australiensis*, *Equisetosporites* [*Ephedripites*] *claricristatus*, *E. lusaticus*, *E. notensis*, *Gamerroites* cf. *psilasaccus*, *Inaperturopollenites hiatus*, *Lygistepollenites florinii*, *Microcachryidites antarcticus*, *Phyllocladidites mawsonii*, *Podocarpidites elegans*, *P.* cf. *ellipticus*, *P.* cf. *exiguus*, *P. marwickii*, *P. rugulosus*. Angiosperms (monocotyledons): *Arecipites subverrucatus*, *Graminidites* (Gramineae), *Milfordia argentina*, *Sparganiaceaepollenites barungensis* [Sparganiaceae]. Angiosperms (dicotyledons): *Acaciapollenites myriosporites*, *Baumannipollis variaperturatus* [Malvaceae], *Canthiumidites* aff. *bellus*, *Chenopodipollis chenopodiaceoides*, *Corsinipollenites atlantica* [Onagraceae], *Cupanieidites reticularis* [Sapindaceae], *Dryadopollis minima*, *Haloragacidites trioratus*, *Intratriporopollenites*, *Malvacipolloides comodoroensis*, *Margocolporites tenuireticulatus*, *M. vanwijhei*, *Milfordia argentina*, *Myrtaceidites verrucosus* [Myrtaceae], *Nothofagidites acromegacanthus*, *N. americanus*, *N. dorotensis*, *N. flemingii*, *N. saraensis*, *N. tehuelchesii* [Fagaceae], *Nyssapollenites endobalteus* [Euphorbiaceae], *Poluspissusites puntensis*, *Polyadopollenites*, *Proteacidites obscurus* [Proteaceae], *P. pseudomoides*, *Pseudowinterapollis couperi* [Winteraceae], *Psilatricolporites operculatus* [Euphorbiaceae, *Alchornea*], *Quintiniapollis striatulosa*, *Retitricolporites cienaguensis*, *Rhoipites baculatus*, *R. cienaguensis*, *R. romeroi*, *Senipites patagonica* [Symplocaceae, *Symplocos*], *Striatricolporites gamerroi*, *Tricolpites reticulatus*, *T. trioblatus*, *Triorites minor*, *Tubulifloridites antipodica* [Compositae], *T. viteauensis* [Compositae]

[Many of the above and the following additions occur in sediments from the San Jorge Gulf area, Santa Cruz Province, in an unnamed unit 1 related to the San Julián Formation of late Oligocene age (not correlated with the Chenque [early Miocene] Formation), and an unnamed unit 2 related to the Monte León Formation of early Miocene age (correlated with the lower part of the Chenque Formation; Barreda & Palamarczuk, 2000a, b]—Ferns and allied groups: *Densoisporites*, *Regulatisporites mallatus*, *Verrucosisporites kopukeunsis*. Gymnosperm: *Trisaccites microsaccatum*. Angiosperms (monocotyledons): *Cyperaceaepollis neogenicus* (Cyperaceae), *Liliacidites*. Angiosperms (dicotyledons): *Clavatipollenites*, *Diporites aspis*, *Ericipites*, *Mutisiapollis viteauensis* (Compositae), *Rubipollis oblatus*

[Many of the above and the following additions occur in sediments from the Continental Platform, Patagonia, late Oligocene–Miocene; Barreda & Palamarczuk, 2000b]—Angiosperms (dicotyledons): *Glenopollis ornatus*, *Striasyncolpites laxus*

Chile

Cretaceous

Megafossils

[53, Cerro Guido, Magallanes Province, southern Chile, formation?, Maastrichtian]

Ferns and allied groups: *Hymenophyllum priscum* (Hymenophyllaceae), *Thyrsopteris antiqua* (Dicksoniaceae; affinities cited as with *Thyrsopteris*, represented in the modern flora by a single species, *T. elegans*, endemic to the Juan Fernández Islands). Gymnosperms: *Acmopyle antarctica* (Podocarpaceae), *Podocarpus inopinatus* (Podocarpaceae), *Pseudoaraucaria valentini* (Araucariaceae)

[54, mostly southern Chile, formation?, ~Late Cretaceous–Eocene?]

Gymnosperms: *Araucarioxylon doeringii*, *A. kellerense*, *A. ohzuanum*, *A. parachoshiense*, *A. pichasquense*, *A. pseudoparenchymatosum*, *A. quiriquineanum*, *Cupressinoxylon mochaense* (Podocarpaceae), *C. parenchymatosum*, *Phyllocladoxylon antarcticum*, *P. aparenchymatosum*, *Podocarpoxylon palaeoandinum*, *P. palaeosalignum* (Podocarpaceae, *Podocarpus*), *Taxodioxylon pseudocompressum*. Angiosperms (dicotyledons): *Acacioxylon pseudocavenium* (Leguminosae, *Acacia*), *Amomyrtoxylon palaeolumum* (Myrtaceae, *Amomyrtus*), *Chilechicoxylon microporosum* (Rosaceae?), *Doroteoxylon vicente-perezii*, *Escallonioxylon palaeoargutum* (Escalloniaceae, *Escallonia*), *Gomortegoxylon patagonicum*, *Gonzalezoxylon mochaense*, *Laurelioxylon intermedium* (Antherospermataceae–Mominiaceae, *Laurelia*), *Laurinium beilschmiedioides* (Lauraceae), *Laurinoxylon uniseriatum* (Fagaceae?), *Myrceugenelloxylon pseudoapiculatum* (Myrtaceae, *Myrceugenella*), *Nothofagoxylon antarcticum*, *N. ohzuanum*, *N. pseudoobliqum*, *N. scalariforme*, *Paragonzar(l)ezoxylon chilenomesozoicum*, *Proteoxylon patagonicum* (Proteaceae), *Ulminium*

Microfossils

[55, Quiriquina Island, Quiriquina Formation, late Senonian or Maastrichtian, Late Cretaceous]

[Some affinities cited are too narrow (e.g., Polypodiaceae for *Polypodiidites*, possibly Liliaceae for *Liliacidites*), and others are unlikely (*Pinus*, *Tsuga*, *Picea*, *Betulaceae*, *Salix*, or *Platanus*) for the Maastrichtian of Chile.]

Ferns and allied groups: *Cyathidites australis*, *C.* cf. *minor* (Cyatheaceae), *Deltoidospora quiriquinaensis*, *Duplosporis*, *Laevigatosporites dehiscens*, *Leiotriletes*, *Polypodiidites inangahuensis*, *Punctatosporites*, *Quiriquinaspora chilensis*, *Trilites* cf. *parvallatus*. Gymnosperms: *Inaperturopollenites laevigatus*, *Parvisaccites* cf. *radiatus*, *Phyllocladidites mawsoni* (Podocarpaceae, *Dacrydium*), *Piceaepollenites*, *Pinuspollenites concepcionensis*, *Podocarpidites multesimus* (Podocarpaceae), *Trisaccites microsaccatus*, *Tsugaepollenites mesozoicus*. Angiosperms (monocotyledons): *Liliacidites variegatus*, *Monocolpopollenites* (Palmae). Angiosperms (dicotyledons): *Beaupreaidites*, *Clavatipollenites hughesii*, *Nothofagidites* (*Nothofagus*), *Proteacidites minor* (Proteaceae), *Retitricolporites*, *Syncolporites*, *Triatriopollenites maedae*, *Tricolpites microreticulatus*, *Tricolpopollenites fallax*, *Tricolporopollenites microporifer*, *T. minor*, *T. punctulosus*, *Triporopollenites festatus*, *T. shimensis*

Paleocene

Microfossils

[56, Bassin d'Arauco–Concepción, Curanilahue Formation (?), Paleocene]

Ferns and allied groups: *Alsophilidites kerguelensis*, *Baculatisporites comaumensis* (Osmundaceae), *Cyathidites australis*, *C. minor* (Cyatheaceae), *Gleicheniidites argentinus*, *G. circinidites* (Gleicheniaceae), *Laevigatosporites ovatus*, *Peromonolites* cf. *bowenii*, *Schizosporis paleocenicus*, *S. rugulatus*. Gymnosperms: *Araucariacites australis* (Araucariaceae), *Cycadopites adjectus*, *C. nitidus* (Cycadaceae), *Dacrydiumites florini*(*i*) (Podocarpaceae, *Dacrydium*), *Ephedripites notensis* (Ephedraceae), *Microcachryidites antarcticus* (Podocarpaceae, *Microcachrys*), *Monosulcites minimus* (Cycadaceae), *Podocarpidites otagoensis* (Podocarpaceae), *Spheripollenites psilatus*, *Trisaccites microsaccatus*. Angiosperms (monocotyledons): *Liliacidites kaitangataensis* (Liliaceae?), *Psilamonocolpites medius* (Palmae). Angiosperms (dicotyledons): *Caryophyllidites polyoratus*, *Casuarinidites coenozoicus* (*cainozoicus*) (Casuarinaceae, *Casuarina*), *Cupaneidites reticularis* (Sapindaceae), *Malvacipollis diversus* (Malvaceae, *Hoheria*), *Myrtaceidites eugenioides*, *Proteacidites amolosexinus*, *P. crassus* (Proteaceae), *P. parvus*, *Psilastephanocolporites fissilis*, *Psilatricolpites coprosmoides* (Rubiaceae, *Coprosma*), *P. fissilis*, *P. minutus*, *Psilatricolporites*, *Retitricolpites microreticulatus*, *Rugutricolporites felix*, *Schizosporis paleocenicus*, *S. rugulatus*, *Tiliaepollenites notabilis* (*Tilia* [?]), *Triorites edwardsii*, *T. harrisii*, *T. minor*, *T. minutipori*

Eocene, Eocene/Oligocene

Megafossils

[57, Quinamávida, Séptima region, Colbún Formation, early Eocene]

Ferns and allied groups: *Blechnum* (Blechnaceae). Gymnosperm: *Podocarpus inopinatus* (Podocarpaceae). Angiosperms (dicotyledons): *Aiouea* (Lauraceae),

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

?*Anacardium* (Anacardiaceae), *Azara* (Flacourtiaceae), ?*Camphoromoea speciosa* (Lauraceae), *Citronella* (Icacinaceae), *Cryptocarya* (Lauraceae), *Cupania romeroi*, *C.* cf. *vernaliformis* (Sapindaceae), *Gaultheria* (Ericaceae), *Leguminosites* (Leguminosae), *Myrcia deltoidea* (Myrtaceae), cf. *Myrtiphyllum bagualense* (Myrtaceae), *Nectandra prolifica* (Lauraceae), *Phoebe elliptica* (Lauraceae), *Rapanea* (Myrsiniaceae), *Rhus* [Anacardiaceae], *Schinopsis* (Anacardiaceae), cf. *Senna* (Leguminosae, *Cassia*), *Tecoma* (Bignoniaceae), *Zizyphus* (Rhamnaceae). Incertae sedis: *Phyllites* (sp. 1–4)

[58, Arauco–Concepción, Curanilahue Formation, Lota and Coronel members, Miocene (Berry, 1922a), Paleocene (Palma-Heldt, 1980b), early Eocene (see Romero, 1986, p. 453; see Table 7.2, Ref. 19a)]

Algae: *Chondrites subsimplex*. Ferns and allied groups: *Adiantites borgoniana*, *Blechnum antediluvianum*, *Cyathoides thyrsopterioides*, *Pecopteris buhsei*, *Pteris cousiniona*. Gymnosperms: *Araucaria araucoensis* (Araucariaceae), *Ephedra* (Gnetaceae; doubtful), *Sequoia chilensis* (Taxodiaceae [?; Berry, 1922a believed the abundant specimens represented the extant genus *Sequoia*]), *Zamia tertiaria* (Cycadaceae). Angiosperms (monocotyledons): *Iriartites* (Palmae), *Sabal ochseniusi* (Palmae). Angiosperms (dicotyledons): *Acrodiclidium oligocaenicum* (Lauraceae), *Aleurites* (?) *platanoides* (Euphorbiaceae), *Allemanda crassostipitata* (Apocynaceae), *Ampelodaphne grandifolia* (Lauraceae), *An(n)ona coronelensis* (Annonaceae), *Antidaphne* (?) *lotensis* (Loranthaceae), *Apocynophyllum chilense* (Apocynaceae), *Ardisia crassifolia* (Myrsinaceae), *Artanthe geniculatoides* (Piperaceae), *Banara cuadare* (Flacourtiaceae), *Bignonia gigantifolia* (Bignoniaceae), *Bombaciphyllum opacum* (Bombaceae), *Bombax firmifolium* (Bombacaceae), *Camphoromoea speciosa* (Lauraceae), *Casearia oliganthoides*, *C. piparoides*, *C. spinulosa-serrata* (Flacourtiaceae), *Cassia gardneri*, *C. longifolia*, *C. oxleyi* (Leguminosae), *Combretum oblongifolium* (Combretaceae), *Copaifera reticulata* (Leguminosae), *Cordia pulchra* (Boraginaceae), *Coussapoa* (?) *quinquenervis* (Moraceae), *Coussarea membranacea* (Rubiaceae), *Desmodium obliquim* (Leguminosae), *Doliocarpus oblongifolia*, *D.* (?) *serrulata* (Dilleniaceae), *Empedoclea repando-serrata* (Dilleniaceae), *Erythrochiton grandifolium* (Rutaceae), *Erythroxylon reichei* (Erythroxylaceae), *Goeppertia engelhardti*, *G. ovalifolia*, *G. spectabilis* (Lauraceae), *Gouatteria tenuinervis* (Rubiaceae), *Haemadictyon tenuifolium* (Apocynaceae), *Hoffmannia protogaea* (Rubiaceae), *Ilex subtilinervis* (Aquifoliaceae), *Laetia transversinervis* (Flacourtiaceae), *Laurophyllum actinodaphnoides* (Lauraceae), *Lecythis neriifolia* (Lecythidaceae), *Leguminosites copaiferaeoides*, *L. erythrinoides* (Leguminosae), *Maytenus araucensis*, *M. magnoliaefolia* (Celastraceae), *Mespilodaphne longifolia* (Lauraceae), *Moschoxylun falcatum*, *M. tenuinerve* (Meliaceae), *Myrcia costatoides*, *M. deltoidea*, *M. nitens*, *M. reticulato-venosa* (Myrtaceae), *Myrciaria acuminata* (Myrtaceae), *Myrciophyllum ambiguaeoides* (Myrtaceae), *Myristica* (?) *fossilis* (Myristicaceae), *Nectandra chilana* (Lauraceae), *Omphales[a] filiciformis* (Euphorbiaceae), *Ouratea* (*Gomphia*) *firmifolia* (Ochnaceae), *Patrisia eocenica* (Flacourtiaceae), *Persea macrophylloides*, *P. microphylla* (Lauraceae), *Phoeba elliptica*, *P. lanceolata* (Lauraceae), *Pilocarpus saavedrai* (Rutaceae), *Psidium membranaceum* (Myrtaceae), *Psittacanthus crassifolius* (Loranthaceae), *Psychotria grandifolia* (Rubiaceae), *Sabicea* (?) *elliptica* (Rubiaceae), *Sapindus acuminatus* (Sapindaceae), *Styrax coriacea*, *S. glabratoides* (Styracaceae), *Tecoma serrata* (Bignoniaceae), *Tetracera elliptica*, *T. rhamnoides* (Dilleniaceae), *Tetraplandra longifolia* (Euphorbiaceae), *Thevetia angustifolia* (Apocynaceae), *Thouinia philippii* (Sapindaceae), *Ticorea foetidoides* (Rutaceae), *Triumfetta irregulariter-serrata*, *T. miocenica* (Tiliaceae), *Vochysia dura* (Vochysiaceae), *Zanthoxylon inaequabile*, *Z. tenuifolium* (Rutaceae). Incertae sedis: *Carpolites cycaeformis*, *C. guilielmaeoides*, *Phyllites acutoserratus*, *P. alsodeiaeoides*, *P. aspidospermaeoides*, *P. banisteriaeoides*, *P. coccolobaefolia*, *P. repandus*, *P. sauraujaeoides*, *P. ternstroemiaeoides*, *P. triplarioides*

Microfossils

[59, Arauco–Concepción, Lota Member, Curanilahue Formation, early Eocene]

Fungi: *Dicellaesporites*, *Granatisporites*, *Inapertisporites*, *Lacrimasporonites*, *Monoporisporites*, *Multicellaesporites*, *Pluricellaesporites*. Bryophyta: *Sphagnum*?. Ferns and allied groups: *Clavifera*, *Cyathidites australis*, *C. minor*, *Gleicheniidites*, *Laevigatosporites*, *Leiotriletes*, *Peromonolites*. Gymnosperms: *Araucariacites*?, *Podocarpidites*, *Trisaccites*. Angiosperms (monocotyledons): *Monosulcites*, *Psilamonocolpites*. Angiosperms (dicotyledons): *Cupaneidites*, *Diporites*, *Haloragacidites harrisii*, *Myrtaceidites*, *Polyporina*, *Proteacidites*, *Psilatricolporites*, *Retitricolporites*, *Tricolpites*, *Tricolporites*

[60, Valley Río Leña Dura, Magallanes Province, Leña Dura Formation, Eocene]

Ferns and allied groups: *Cyatheacidites annulatus* (Cyatheaceae), *Trilites*, *T. tuberculiformis* (Dicksoniaceae?). Gymnosperm: *Phyllocladidites mawsonii* (Podocarpaceae, *Dacrydium*). Angiosperms (dicotyledons): *Nothofagus brassii* group, *N. fusca* group (Fagaceae), Proteaceae

[61, Lonquimay, Araucanía Region, Malleco Province, Lonquimay Formation, Eocene–middle Oligocene (Miocene?); cf. Ref. 59]

Fungi: *Dicellaesporites*, *Didymoporisporonites*, *Granatisporites*, *Inapertisporites*, *Lacrimasporonites*, *Monoporisporites*, *Multicellaesporites*, *Pluricellaesporites*. Algae: *Botryococcus braunii*. Ferns: *Cyathidites australis*, *C. minor*, *C. patagonicus*, *Laevigatosporites vulgaris*, *Polypodium* type, *Verrucosisporites*. Gymnosperms: *Araucariacites* cf. *australis*, *Podocarpidites* cf. *marwickii*, *P.* cf. *otagoensis*, *Trisaccites microsaccatum*. Angiosperms (monocotyledon): *Monocolpites*. Angiosperms (dicotyledons): Composite type [age too uncertain for valid report], Malvaceae type [age too uncertain], *Myrtaceidites*, *Nothofagidites cincta*, *N. mensiesii* group (Fagaceae), *Proteacidites*, Sapindaceae type [age too uncertain], *Tricolpites*, *Tricolporites microreticulatus*

Oligo–Miocene

Megafossils

[62, Guadal area, Aisén Region, Guadal and Río Zeballos formations, Oligo–Miocene/Miocene]

Ferns and allied groups: *Equisetum* (Equisetaceae). Angiosperm (dicotyledon): *Nothofagus* cf. *densinervosa*

Microfossils

[63, Mina Ligorio Márquez, Guadal Formation, Oligo–Miocene]

Ferns and allied groups: Trilete spore. Gymnosperm: *Podocarpidites*. Angiosperms (dicotyledons): *Carya* type (Juglandaceae), Compositae type, *Myrtaceidites*, *Nothofagidites*; various other unnamed forms referred to Proteaceae type

[64, Arauco–Concepción, Lota Member, Curanilahue Formation, Eocene–Oligocene]

Fungi: *Dicellaesporites*, *Granatisporites*, *Inapertisporites*, *Lacrimasporonites*, *Monoporisporites*, *Multicellaesporites*, *Pluricellaesporites*. Ferns and allied groups: *Clavifera*, *Cyathidites minor*, *Gleichenidiites*, *Laevigatosporites*, *Leiotriletes*, *Peromonolites*. Gymnosperm: *Podocarpidites*. Angiosperms (monocotyledon): *Psilamonocolpites*. Angiosperms (dicotyledons): *Cupaneidites*, *Diporites*, *Haloragacidites harrisii*, *Myrtaceidites*, *Proteacidites*, *Retitricolporites*, *Tricolpites*

Bolivia

Late Cretaceous–Paleocene

Microfossils

[65, vicinity of Ríos Flora–Madidi–Linavijaja, northwest of La Paz, Eslabón (late Maastrichtian) and Flora (Paleocene) formations]

Algae: *Botryococcus braunii*. Ferns and allied groups: *Azolla*, *Calamospora mesozoica*, *Cyathidites*, *Gabonisporis vigourouxii*, *Gemmatriletes clavatus*. Gymnosperms: *Araucariacites australis*, *Classopollis*, *Ephedripites ba[r]gho[o]rnii*, *E. jansonii*, *E. montanaensis*, *E. strigatus*, *Monosulcites minimus*, *Spheripollenites* cf. *psilatus*, *Taxodiaceapollenites* cf. *hiatus*. Angiosperms (monocotyledon): *Mauritidiites franciscoi* [Palmae]. Angiosperms (dicotyledons): *Proteacidites dehaani*, *Psilaperiporites bolivensis*, *P. suarezi*, *Psilatricolpites divisus*, *Retimonocolpites*, *Retitricolpites retiaphelis*, *Retitricolporites microreticulatus*, *Sofreipites*, *Spinozonocolpites*, *Striatricolpites*, *Syncolporites poricostatus*, *Tetradites*, *Tricolpites synstriatus*, *Tricolporites*, *Tricornites elongatus*, *Triorites*, *Triporotetradites gemmatus*, *Ulmoideipites krempii*

Eocene–Oligocene

Microfossils

[66, Altiplano, Bolivia, Potoco Formation, late Eocene to early Oligocene; purpose geological, no biological affinities cited]

Algae: *Pediastrum*. Ferns and allied groups: *Chomotriletes fragilis*, *Deltoidospora*, *Echitriletes mulleri*, *Gleicheniidites senonicus*, *Lycopodiumsporites novomexicanum*,

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Osmundacidites, *Perotriletes*, *Polypodiaceoisporites potoniei*, *Verrucatosporites usmensis*. Gymnosperms: *Araucariacites australis*, *Cedridites*, *Podocarpidites*. Angiosperms (monocotyledons): *Monocolpites*, *Monoporites annulatus* [Gramineae]. Angiosperms (dicotyledons): *Acacia* (Leguminosae), *Aesculiidites*, *Bombax* (Bombacaceae), *Echiperiporites akanthos*, *E. estelae* [Malvaceae, larger forms cf. *Hibiscus*], *Jussitriporites* [Onagraceae], *Margocolporites vanwijhei* [Leguminosae, Caesalpinioideae, cf. *Caesalpinia*], *Milfordia minima*, *Psilaperiporites minimus*, *P. robustus*, *Psilatricolpites*, *Psilatricolporites maculosus*, *P. operculatus* [Euphorbiaceae, *Alchornea*], *Retitricolpites americana*, *Retitricolporites amazonensis*, *Scabraperiporites nativensis*, *Spinozonocolpites echinatus*, *Tricolporopollenites hians*, *Ulmoideipites krempii*, *Verrutriporites*, *Zonocostites ramonae* [*Rhizophora*]

Peru

Late Cretaceous

Microfossils

[67, 68, Río Huaya–Río Ucayali, eastern Peru, Vivian Formation, Campanian]

Ferns and allied groups: *Caudaspora spinosa*, *C. verrucata*, *Thecaspora spinosa*, *Zlivisporis*. Angiosperms (monocotyledon?): *Auriculiidites reticulatus*. Incertae sedis: *Cyclusphaera euribei*

Early Eocene

Megafossils

[69, Pariñas District and Paita Province (Belen), northwestern Peru, Pariñas Sandstone, Negritos Formation, Oligocene in Berry (1927), early Eocene in Hoffstetter, 1956 (see Romero, 1986, p. 453)]

Angiosperms (monocotyledon): *Palmocarpon bravoi* (Palmae). Angiosperms (dicotyledons): *Anacardium peruvianum* (Anacardiaceae), *Cupanoides peruvianus* (Sapindaceae), *Leguminosites mucunoides* (Leguminosae), *Saccoglottis cipaconensis* (Humiriaceae), *Sapindoides peruvianus* (Sapindaceae). Incertae sedis: *Carpolithus belenensis*, *C. bravoi*, *C. olssoni*, *C. rutoides*

[70, Punta Pariñas (Belen), formerly in Paita Province, Department Piura, as Ref. 69 above, early Eocene]

Angiosperms (monocotyledons): *Palmocarpon belensis*, *P. bravoi*, *P. cocoides* (Palmae). Angiosperms (dicotyledons): *Ampelocissus bravoi* (Vitaceae), *Anacardium peruvianum* (Anacardiaceae), *An(n)ona peruviana* (Annonaceae), *Cissus willardi* (Vitaceae), *Cucurbites compressus* (Cucurbitaceae), *Cupanoides peruvianus* (Sapindaceae), *Fagara piurana* (Rutaceae), *Ficus sphericus* (Moraceae), *Jatropha tertiaria* (Euphorbiaceae), *Leguminosites belensis*, *L. mucunoides* (Leguminosae), *Lithospermites glabrum* (Boraginaceae), *Malvacarpus octoloculus* (Malvaceae), *Matayba belensis* (Sapindaceae), *Psychotria eogenica* (Rubiaceae), *Saccoglottis cipaconensis* (Humiriaceae), *Sapindoides peruvianus* (Sapindaceae), *Tetracera belensis* (Dilleniaceae), *Uragoga tertiaria* (Rubiaceae), *Vantanea compressiformis* (Humiriaceae), *Virola tertiaria* (Myristicaceae). Incertae sedis: *Carpolithus belenis*, *C. cissiformis*, *C. dicellaformis*, *C. inusitatus*, *C. olssoni*, *C. peruvianus*, *C. rutoides*

[71, Punta Arena, south of Talara Tunnel, NW Peru, Restin Formation (= Chacras Formation, see Ref. 69), early Eocene]

Angiosperms (monocotyledons): *Attalea olssoni* (Palmae), *Iriartites restinensis* (Palmae). Incertae sedis: *Carpolithus jatrophaformis*

Ecuador

Eocene

Megafossils

[72, Ancon Point, Sta. Elena Peninsula, Ancon Sandstone, Eocene]

Angiosperms (monocotyledons): *Palmocarpon bravoi* (Palmae). Angiosperms (dicotyledons): *Anacardium peruvianum* (Anacardiaceae), *An(n)ona peruviana* (Annonaceae), *Sapindoides peruvianus* (Sapindaceae), *Vantanea sheppardi* (Humiriaceae)

Colombia

Cretaceous

Megafossils

[73, Middle Valley, Río Magdalena, Rosa Blanca Formation, Early Cretaceous (Hauterivian?)]

Gymnosperm: *Protophyllocladoxylon rosablancaense* (Podocarpaceae?, in Pons, 1988, fossil wood)

[74, coastal basins, eastern Colombia, Rosa Blanca, Paja, Villavicencio, and Gacheta formations, Early Cretaceous (Barremian–early Cenomanian, see Table 7.2), includes megafossils and microfossils]

Rosa Blanca Formation

Fossil wood: *Protophyllocladoxylon rosablancaense* (Podocarpaceae?)

Paja Formation

Fossil wood: *Metapodocarpoxylon libanoticum* (Podocarpaceae?)

Villavicencio Formation

Megafossils: Ferns and allied groups: *Phlebopteris* (Matoniaceae), *Weichselia reticulata* (see also Berry, 1937d). Gymnosperms: Bennetitales—*Zamites* cf. *tenuinervis*, Coniferales. Incertae sedis: *Cupressinocladus pompeckji*, *Podozamites*. Angiosperm [monocotyledon(?)]: *Monocotylophyllum heterophyllum*. Incertae sedis: *Dicotylophyllum spatulatum*, *D.* sp. A–D, *Moutonia quetamensis*, *M. sinuate*.
Microfossils: Algae (dinoflagellates): *Cometodinium whitei*, *Subtilisphaera*; (Chlorophyta)—*Pterospermella*, *Schizocystia*. Bryophyte: *Aequitriradites baculatus*. Ferns and allied groups: *Apiculatisporis*, *Auritulinasporites* (Gleicheniaceae?), *Baculatisporites comaumensis* (Grammitidaceae), *Biretisporites potoniaei* [author cites morphological similarity to *Odontosoria guatemalensis* (Dennstaedtiaceae) figured by Tryon & Tryon, 1982, p. 40, fig. 12], *Cadiospora* (*Bellisporites*), *Camarozonosporites* (*Lycopodium*), *Chomotriletes minor* (possibly an alga), *Cibotiidites* (Dicksoniaceae), *Cicatricosisporites annulatus* (Schizaeaceae), *C. australiensis*, *C. berouensis*, *C.* cf. *hallei*, *C.* cf. *subrotundus*, *Concavisporites jurienensis*, *Concavissimisporites minor*, *C. punctatus*, *Converrucosisporites saskatchewanensis*, *Cyathidites minor* (*Cyathea*), *Cyclogranisporites*, *Deltoidospora hallii*, *D. juncta*, *Dictyophyllidites harrisii*, *Distaltriangulisporites* cf. *perplexus* (Schizaeaceae), *Divisisporites* cf. *maximus*, *Echinatisporis varispinosus* (*Selaginella*), *Elaterocolpites castelaini*, *Elaterosporites klaszi*, *E. verrucatus*, *Foraminisporis wonthaggiensis*, ?cf. *Gemmatriletes clavatus*, *G.* cf. *densegemmatus*, *Hamulatisporis* (Lycopodiaceae), *Impardecispora trioreticulosa* (Pteridaceae, *Cryptogramma crispa*, Tryon & Tryon, 1982, p. 308), *Klukisporites* (Schizaeaceae, *Lygodium*), *Kraeuselisporis*, *Laevigatosporites*, *Microfoveolatosporis* (Schizaeaceae?), *Minerisporites* (Selaginellaceae, megaspore), *Neoraistrickia* (Selaginellaceae), *Osmundacidites wellmanii* (Osmundaceae), *Punctatisporites* (*Todisporites*) *major* (Osmundaceae), *Punctatosporites scabratus* (Marattiaceae), *Retitriletes* (Lycopodiaceae), *Sergipea*, *Sestrosporites pseudoalveolatus* (Lycopodiaceae, *Lycopodium*), *Uvaesporites* (*Selaginella*), *Verrucosisporites rotundus* (Grammitidaceae). Gymnosperms: *Applanopsis segmentatus* (Podocarpaceae?), *A. trilobatus* (Podocarpaceae), *A. turbatus* (Podocarpaceae?), *Araucariacites australis* (Araucariaceae), *A. guianensis* (Araucariaceae?), *Balmeiopsis limbatus* (Araucariaceae?), *Cerebropollenites macroverrucosus* (Pinaceae, *Tsuga* [?]), *Classopollis*, *Cycadopites minimus* (Cycadales), *C. nitidus*, *Equisetosporites ambiguus* (Ephedrales), *E. costaliferous*, *E. dudarensis*, *E. leptomatus*, *E. mollis*, *E.* cf. *subcircularis*, *E. translucidus*, *Eucommiidites minor*, *Gnetaceaepollenites boltenhagenii* (Ephedrales), *Inaperturopollenites dubius*, *Spheripollenites subgranulatus*, *Trifossapollenites*, nucellus of *Caytonia*. Angiosperms (monocotyledons): *Liliacidites*, *Retimonocolpites dividuus*, *R.* aff. *Clavatipollenites minutus*. Angiosperms (dicotyledons): *Foveotricolpites*, *Inaperturopollenites crisopolensis* (Chloranthaceae?), *Retitricolpites vulgaris*, *Stellatopollis*, *Tetracolpites*, *Tricolpites*. Angiosperms incertae sedis: *Afropollis operculatus*, *Monosulcites*, *Retimonocolpites peroreticulatus*, *Striatricolpites reticulatus* (or Ephedrales). Position unknown: cf. *Reyrea*, *Schizosporis microreticulatus*

Gacheta Formation

Megafossils: Gymnosperms: Cycadales—*Pseudoctenis* (?), Coniferales incertae sedis—*Brachyphyllum*, *Cupressinocladus leptocladoides*, *Podozamaites*. Angiosperms (dicotyledons), incertae sedis: *Cinnamomoides gachetaensis* (author notes no intended affinity with *Cinnamomum*), *Dicotylophyllum* sp. E, *Phyllites*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

Microfossils: Ferns and related groups: *Dictyophyllidites harrisii*, *Distaltriangulisporites* cf. *perplexus* (Schizaeaceae). Gymnosperms: *Applanopsis dampieri* (Podocarpaceae?), *A. trilobatus*, *Araucariacites australis* (Araucariaceae), *Balmeiopsis limbatus* (Araucariaceae?), *Classopollis*, *Cycadopites minimus*. Angiosperm (monocotyledon): *Retimonocolpites* aff. *Clavatipollenites minutus*. Angiosperms incertae sedis: *Afropollis operculatus*, *Monosulcites*, *Retimonocolpites peroreticulatus*

Microfossils

[78d, Santa Maria–San Luis de Gaceno, NE of Bogotá, Une Formation, late Aptian–earliest Cenomanian]

Ferns and allied groups: *Cicatricosisporites venustus*, *Cyathidites–Deltoidospora*, *Elaterocolpites castelaini*, *Elateroplicites africaensis*, *Elaterosporites klaszii*, *Impardecispora*, *Leptolepidites*, *Lycopodiumsporites*, *Perotrilites pannuceus*, *Uvaesporites*. Gymnosperms: *Araucariacites australis*, *Callialasporites dampieri*, *Classopollis*, *Ephedripites barghoornii*, *Eucommiidites minor*, *Inaperturopollenites*, *Monosulcites*. Angiosperms (monocotyledon): *Retimonocolpites*. Angiosperms (dicotyledons): *Afropollis jardinus*, *Cretaceioporites polygonalis*, Psila/scabraticolpates, Reticolpates

[79, Basin de Boyaca, Guaduas Formation, Maastrichtian]

Epiphyllous fungi: *Callimothallus corralesence*, *Molinea asterinoides*

[80, Valle Medio del Magdalena, Cimarrona Formation, Maastrichtian]

Fungi: *Fusiformisporites lineolatus*, *Monoporisporites grandis*. Ferns and allied groups: *Appendiciporites* (Schizaeaceae), *Baculatisporites*? *multibaculae*, *Buttinia andreevi*, *Cibotiidites*, *Cycatheacidites vanderhammeni*, *Deltoidospora*, *Leiotriletes giganteus*, *Lycopodiumsporites* (Lycopodiaceae), *Lygodioisporites* (*Lygodium*?), *Muerrigerisporis americanus* (*Selaginella*), *Reticulatisporites*, *Schizaeoisporites cicatricos*, *S. rectangularis* (Schizaeaceae), *Schizosporis*. Gymnosperms: *Ephedripites*, *Proxapertites*. Angiosperms (monocotyledons): *Baculamonocolpites minimus*, *B. multispinosus*, *Baculamorphomonocolpites tausae*, *Foveomorphomonocolpites* (*Proxapertites*) *humbertoides*, *Liliacidites* (Liliaceae), *Psilamonocolpites medius*. Angiosperms (dicotyledons): *Echimonocolpites minutispinosus* (Nymphaeaceae?), *Ericipites* (Ericaceae), *Magnatriporites umirensis*, *Plicapollis bellus*, *Proteacidites dehaani*, *Psilastephanocolporites*, *Psilatricolpites*, *Retidiporites magdalenensis*, *Retisyncolporites aureus*, *Retitricolpites*, *Retitricolporites*, *Striatricolpites*, *Triporites*, *Verrutricolpites*, *Verrutricolporites*. Incertae sedis: *Classopollis*?, *Dicolpopollis*?

[81, Catatumbo and Cesar basins, northeastern Colombia, Colón Formation, Maastrichtian]

Ferns and allied groups: *Baculatisporites multibaculae*, *Buttinia andreevi*, *Cyatheacidites vanderhammenii*, *Leiotriletes guaduensis*. Gymnosperms: *Araucariacites*, *Ephedripites*, *Inaperturopollenites*, *Proxapertites*. Angiosperms (monocotyledons): *Baculamonocolpites multispinosus*, *Baculamorphomonocolpites tausae*, *Baculatisporites multibaculae*, *Crusafontites grandiosus*, *Monocolpites ruedae*, *Spinozonocolpites baculatus*, *S. echinatus*. Angiosperms (dicotyledons): *Foveomorphomonocolpites* (*Proxapertites*) *humbertoides* (Annonaceae), *Longapertites proxapertitoides*, *Tetradites umirensis*, *Triporites iversenii*, *T. suescae*

[82, Sabana de Bogotá, Guaduas Formation, Maastrichtian–Paleocene]

Ferns and allied groups: *Leiotriletes guaduensis* (Cyatheaceae). Angiosperms (monocotyledons): *Baculamonocolpites multispinosus*, *Baculamorphomonocolpites tausae*, *Crusafontites grandiosus*. Angiosperms (dicotyledon): *Foveomorphomonocolpites* (*Proxapertites*) *humbertoides* (Annonaceae)

[83, Cerrejón Basin, Department of Guajira, Hato Nuevo–Cerrejón formations, late Paleocene]

Epiphyllous fungi: Ascomycetes, hyphae—*Asterinites colombiensis*, *A. tellezii*; dispersed fungal spores—*Dicellaesporites fusiformis*, *D. magnus*, *D. rinconii*, *Diporisporites hammenii*, *Lacrimasporonites arcuatus*, *L. ovalis*, *Monoporisporites perminutus*, *Multicellaesporites cerrejonensis*, *Polyadosporites*

[84, regions of Catatumbo, Lebrija, Tibú, Vanegas, no formations (zones), all Paleocene]

Angiosperms (monocotyledons): *Echimonocolpites ruedae*, *Gemmamonocolpites gemmatus*, *Longaperites proxapertitoides*, *Mauritidites franciscoi* (Palmae, *Mauritia*), *Proxapertites operculatus* (Palmae, *Astrocaryum*; Araceae fide Zetter et al., 2001), *Psilamonocolpites medius* (Palmae), *Retimonocolpites microreticulatus*, *R. regio* (Palmae). Angiosperms (dicotyledons): *Ephedripites vanegensis* (Araceae, *Spathiphyllum*), *Foveotricolpites perforatus*, *F. pomarius*, *F. santanderianus*, *Gemmastephanocolpites gemmatus*, *Heterocolpites palaeocenica*(*us*) (Melastomataceae), *Magnotetradites magnus*, *Proxapertites tertiaria* (Annonaceae), *Psilatricolpites palaeocenica*, *Retidiporites magdalenensis*, *Retitricolpites herrerae*, *R. microreticulatus*, *Retitricolporites* (*Bombaccidites*) *annae* (Bombacaceae), *R. annaeoides* (= *B. annae*), *Scabrastephanocolpites lisamae*, *S. scabratus*, *S. vanegensis*, *Syncolporites lisamae*, *Verrustephanocolpites verrucatus*

[75, Arroyo Mancamajor–Ovejas, Department of Bolívar; Zipacón, Cundinamarca Province; no formation, age? (Eocene, Oligocene)]

Angiosperms (dicotyledons): *Anacardium eocenicum* (Anacardiaceae), *Vantanea columbiana* (Humiriaceae)

[76, Pijaquay Department of Bolívar, formation?, middle Eocene]

Angiosperm (dicotyledon): *Celtis bolivarensis* (Ulmaceae)

[77, Zipacón, Cipacón, and páramo of Guasca, Cundinamarca Province, formation?, late Eocene–Oligocene]

Angiosperms (dicotyledons): *Cordia vera* (Boraginaceae), *Saccoglottis cipaconensis* (Humiriaceae), *Simaruba versicoloroides* (Simarubaceae)

[78a, Ituango, Department of Antioquia, Cordillera Occidental, formation?, Eocene]

Angiosperm (dicotyledon): *Melastomaceophyllum danielis* (Melastomataceae)

Late Oligocene–Early Miocene

Megafossils

[78b, Planeta Rica, Córdoba, eastern San Jeronimo, formation?, Oligo–Miocene]

Angiosperm (dicotyledon): *Lecythidospermum bolivarensis* (Lecythidaceae)

[78c, Antioquia Basin, central valley of the Río Cauca, Department Antioquia, Antioquia Formation, late Oligocene–early Miocene]

Angiosperms (dicotyledons): *Anacardioxylon caracoli* (Anacardiaceae), *Guttiferoxylon compactum* (Guttiferae, Clusiaceae), ?*Leguminoxylon grossei* (Leguminosae), *Sapindoxylon antioquiense* (Sapindaceae), *Terminalioxylon* cf. *naranjo* (Combretaceae)

Microfossils

[85, Llanos foothills, southern Catatumbo, northern Middle Magdalena (Eastern Andes), San Fernando (middle Eocene), Arcillas de El Limbo (late Paleocene), La Paz (early to middle Eocene), Areniscas de El Limbo (early to middle Eocene), Mirador (early to middle Eocene); see also Pardo-Trujillo et al., 2003 for additions from the Lisama and La Paz formations (early to middle Eocene) formations]

Ferns and allied groups (possibly some bryophytes): *Apiculatasporites* (?) *cingulatus*, *A. obscurus*, *Baculatisporites*, *Camarozonosporites*, *Chomotriletes minor*, *Cicatricosisporites dorogensis* (Schizaeaceae), *Cicatricoso*[*i*]*sporites decussatus*, *C. eocenicus*, *Clavatisporites mutisii*, *Echinatisporis brevispinosus*, *Foveotriletes margaritae*, *Ischyosporites problematicus*, *Kirchheimerisporites tenuiradiatus*, *Laevigatosporites tibuensis*, *L.* sp., *Microfoveolatosporis skottsbergii*, *Osmundacidites minor*, *Planisporites*, *Polypodiaceoisporites*? *fossulatus*, *Polypodiisporites echinatus*, *P.* aff. *inangahuensis*, *P. pachyexinatus*, *P.* aff. *speciosus*, *Pteridacidites*, *Retitriletes*, *Scabramonoletes* (?), *Tuberositriletes verrucatus*, *Zlivisporis blanensis*. Gymnosperms: *Araucariacites*, *Ephedripites vanegensis* (*Ephedra*). Angiosperms (monocotyledons): *Aglaroeidia*? *foveolata*, *Arecipites regio* (Palmae), *Baculamonocolpites hammenii*, *Bacumorphomonocolpites tausae*, *Clavamonocolpites*, *Curvimonocolpites inornatus*, *Echimonocolpites*, *Gemmamonocolpites gemmatus*, *G. perfectus*, *Longapertites microfoveolatus* (Palmae, *Eremospatha*), *L. proxapertitoides*, *Luminidites colombianensis* (Palmae, *Phytelephas*), *Mauritiidites franciscoi* (Palmae, *Mauritia*), *Monocolpopollenites ovatus*, *Monoporopollenites annulatus* (Gramineae–Poaceae), *Proxapertites cursus*, *P. operculatus* (Palmae), *P. psilatus*, *P. verrucatus* (Palmae), *Psilamonocolpites grandis*, *P. medius* (Palmae), *Racemonocolpites facilis*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

(Palmae, *Iriartea* type), *R. racematus*, *Spinizonocolpites* aff. *baculatus* (Palmae, *Nypa*), *S. breviechinatus*, *S. grandis*, *S. pachyexinatus*. Angiosperms (dicotyledons): *Albertipollenites? perforatus*, *Araliaceoipollenites*, *Bacutriporites echinatus*, *Bombacacidites annae* (Bombacaceae), *B. brevis*, *B. fossureticulatus*, *B. foveoreticulatus*, *B. gonzalezii*, *B. grahamii*, *B. nacimientoensis*, *B. protofoveoreticulatus*, *B. psilatus*, *B. simplireticulatus*, *B. soleaformis* [all cf. Bombacaceae], *Brevitricolpites macroexinatus*, *B. microechinatus*, *Clavatricolpites densiclavatus*, *Colombipollis tropicalis*, *Corsinipollenites psilatus* [Onagraceae], *C. undulatus* (Onagraceae, *Jussiaea* type), *Cricotriporites elongatoporus*, *C. guianensis*, *C. macroporus*, *C. minutiporus*, *Crototricolpites* cf. *annemariae*, *C. protoannemariae*, *Crusafontites megagemmatus*, *Ctenolophonidites cruciatus* (Ctenolophonaceae?), *Duplotriporites ariani*, *Echiperiporites estelae* (Malvaceae, *Thepesia*, *Hibiscus*), *Echitetracolpites? tenuiexinatus*, *Echitricolpites*, *Echitriporites trianguliformis* (Proteaceae?), *E. variabilis*, *Foveodiporites guianensis*, *Foveotricolpites perforatus*, *Foveotricolporites fossulatus*, *F. rugulatus*, *Foveotriporites hammenii*, *Horniella*, *Jandufouria minor*, *Ladakhipollenites rubinii*, *L. simplex*, *Lakiapollis* aff. *ovatus* (Malvaceae), *Lanagiopollis crassa* (Pelliceriaceae, *Pelliceria*), *Lymingtonia?*, *Margocolporites vanwijhei* (Leguminosae), *Momipites africanus*, *Multiporopollenites pauciporatus*, *Nothofagidites huertasii* [Fagaceae], *Paleosantalaceaepites distinctus*, *Parsonsidites*, *Perfotricolpites digitatus* (Convolvulaceae, *Merremia*), *Periretisyncolpites giganteus*, *Perisyncolporites pokornyi* (Malpighiaceae), *Poloretitricolpites absolutus*, *Propylipollis pseudocostatus* (Proteaceae), *Proxapertites humbertoides* (Annonaceae, *Malmea*), *P. magnus*, *Psilabrevitricolpites*, *Psilabrevitricolporites simpliformis*, *P. triangularis*, *Psilastephanocolpites*, *Psilastephanocolporites brevicolpatus*, *P. fissilis* (Polygalaceae), *Psilastephanoporites*, *Psilasyncolporites*, *Ranunculacidites operculatus* (Euphorbiaceae, *Alchornea*), *Retibrevitricolpites retibolus*, *R. triangulatus*, *Retibrevitricolporites grandis*, *R. speciosus*, *Retidiporites elongatus*, *R. magdalenensis* (Proteaceae), *R. poricostatus*, *Retipollenites*, *Retistephanocolpites angeli*, *R. fossulatus*, *Retistephanocolporites festivus*, *R. fossulatus*, *Retistephanoporites angelicus*, *R. crassiexinatus*, *R. minutiporus*, *Retisyncolporites angularis*, *Retitrescolpites baculatus*, *R.? irregularis* (Euphorbiaceae), *R. magnus*, *R. peculiaris*, *R. saturum*, *Retitriporites amplireticulatus*, *R. poricostatus*, *Rhoipites cienagensis*, *R. guianensis* (Sterculiaceae/Malvaceae), *R. hispidus*, *R. squarrosus*, *Rousea florentina*, *Rugotricolporites felix*, *Scabrastephanocolpites*, *Siltaria mariposa*, *S. media*, *Spirosyncolpites spiralis*, *Striatopollis catatumbus* (Leguminosae, *Crudia* type), *S. minor*, *S.? tenuistriatus*, *Striatricolporites digitatus*, *Syncolporites lisamae* (Myrtaceae), *S. marginatus*, *Tetracolporites pachyexinatus* (Meliaceae?), *T. psilatus*, *Tetracolporopollenites maculosus* (Sapotaceae, *Chrysophyllum*), *T. spongiosus*, *T. transversalis*, *Tricolpites antonii*, *T. clarensis*, *T. protoclarensis*, *Triporopollenites? tenuiexinatus*, *Ulmoideipites krempii* (Ulmaceae), *Venezuelites? distinctus*, *Verrustephanocolpites rugulatus*, *Verrustephanoporites*, *Verrutricolpites*, *Verrutricolporites reticulatus*, *Wilsonipites margocolpatus*, *Zonocostites minor*

[86, Tibú area, upper Catatumbo drainage, Colombia–Venezuela border, Los Cuervos and Mirador formations, lower and middle Eocene; new species only]

Ferns and allied groups (trilete and monolete spores) present but not treated in this publication. Angiosperms (monocotyledons): *Clavamonocolpites terrificus*, *Echimonocolpites densus*, *Echimorphomonocolpites gracilis*, *E. solitarius*, *Gemmamonocolpites amicus*, *G. barbatus*, *G. ovatus*, *Longitrichotomocolpites triangularis*, *Monoporites annuloides* (*Monoporopollenites annulatus*; Gramineae), *Papillamonocolpites splendens*, *Racemonocolpites facilis*, *R. racematus*, *R. romanus*, *Retimonocolpites bernardii*, *R. splendidus*, *R. tertiarius*. Angiosperms (dicotyledons): *Annutriporites iversenii*, *Arcotriporites asteroides*, *Bacustephanocolpites stereos*, *Brevitricolpites variabilis*, *Clavatricolpites gracilis*, *Echitriporites trianguliformis*, *Ericipites annulatus* (Ericaceae), *Foveotricolpites genuinus*, *Foveotricolporites caldensis*, *F. marginatus*, *F. voluminosus*, *Foveotriporites hammenii*, *Gemmastephanoporites breviculus*, *G. polymorphus*, *Gemmatricolpites pulcher*, *Heterocolpites paluster* (Melastomataceae), *Jussitriporites undulatus* (Onagraceae, *Jussiaea*), *Longapertites brasiliensis* (Annonaceae type), *L. circulatus*, *L. fossuloides*, *L. perforatus* (Annonaceae type), *L. proxapertitoides*, *Magnaperiporites spinosus*, *Magnatriporites abstractus*, *Papillopollis partialis*, *Perfotricolpites digitatus*, *P. semistriatus*, *Plicapollis arcii*, *Polotricolporites concretus*, *P. mocinnii*, *P. versabilis*, *Pseudostephanocolpites perfectus*, *P.(?) verdi*, *Psiladiporites redundantis*, *Psilastephanocolpites adinos*, *P. marginatus*, *P. verrucosus*, *Psilasyncolporites parvus*, *Psilatricolpites acerbus*, *P. brevis*, *P. minutus*, *P. polaroides*, *P. simplex*, *Psilatricolporites normalis*, *P. obscurus*, *P. operculatus*, *P. optimus* (Euphorbiaceae, *Alchornea*), *P. vanus*, *Retibrevitricolpites catatumbus*, *R. increatus*, *R. triangulatus*, *Retidiporites agilis*, *Retiheterocolpites tertiarius*, *Retistephanocolpites angelicus* (Bombacaceae, *Catostemma*), *R. finalis*, *R. minutus*, *Retistephanocolporites festivus*, *Retistephanoporites angelicus*, *Retisyncolporites angularis*, *R. aureus*, *Retitricolpites absolutus*, *R. adeptus*, *R. adultus*, *R. antonii*, *R. bonus*, *R. clarensis*, *R. conciliatus*, *R. constrictus*, *R. florentinus*, *R. incisus*, *R. magnus*, *R. maledictus*, *R. maturus*, *R. minutus*, *R. perditus*, *R. perforatus*, *R. saturum*, *R. simplex*, *Retitricolporites craceus*, *R. equatorialis*, *R. finitus*, *R. hispidus*, *R. irregularis*, *R. marianis*, *R. medius*, *R. profundus*, *R. saskiae*, *Retitriporites dubiosus*, *R. federicii*, *R. tilburgii*, *R. typicus*, *Rugutricolporites felix*, *Scabratricolpites tibialis*, *Scabratriporites moderatus*, *S. redundans*, *Semitectotriporites gratus*, *Spirosyncolpites clavatus*, *S. spiralis*, *Striatricolpites catatumbus* [Leguminosae, *Crudia* type], *S. semistriatus*, *Striatricolporites angustinus* (cf. Anacardiaceae), *Verrutricolpites irregularis*, *V. unicus*, *Verrutricolporites haplites*. Incertae sedis: *Classites capucinii*, *Clavainaperturites cordatus*, *Echinoidites problematicus*, cf. *Ephedripites*, *Retipollenites confusus*

[87, Amaga Basin, Cordillera Central, west of Medellín, formation?, Eocene–Oligocene?]

Ferns and allied groups: *Intrapunctosporis semipunctus*, *Laevigatosporites discordatus*, *L. nutidus*, *Verrucatosporites usmensis*. Angiosperms (monocotyledons): *Mauritiidites franciscoi* (Palmae), *Monocolpites medius* (Palmae). Angiosperms (dicotyledons): *Psilatricolporites amagensis*, *P. molinae*, *Retistephanoporites angelicus*, *Retitricolpites maledictus*, *R. vetteri*, *Retitricolporites irregularis*, *R. medius*, *Spirosyncolpites spiralis*, *Striatricolpites catatumbus* [Leguminosae, *Crudia* type]

Venezuela

Early Cretaceous

Microfossils

[90, Zuata Well area (MARAVEN), eastern Venezuela, formation?, Early Cretaceous, ?Aptian–early Albian]

Ferns and allied groups: *Biretisporites* cf. *potoniaei*, *Callialasporites dampieri*, *Cicatricosisporites australiensis*, *C. avnimelechi*, *C. dorogensis*, *C. patomacensis*, *C. recticiatricosus*, *C. subrotundus*, *Cingulatisporites verrucatus*, *Concavisporites*, *Contignisporites fornicatus*, *Coptospora*, *Cyathidites australis*, *C. minor*, *Dictyophyllidites equiexinus*, *Foveotriletes*, *Gleicheniidites apilobatus*, *Hamulatisporis hamulatis*, *Klukisporites variegatus*, *Leptolepidites major*, *L. verrucatus*, *Lycopodiumsporites paleocenicus*, *Monosulcites*, *Perotriletes pannuceus*, *Retimonocolpites*, *Schizaea certa*, *S. reticulata*, *Sergipea naviformis*, *Velosporites*, *Verrucosisporites*, *Zonalapollenites* [?, spore]. Gymnosperms: *Classopollis jardinei*, *C. obidosensis*, *C. torosus*, *Ephedripites ambonoides*, *E. barghoornii*, *E. procerus*, *E. strigatus*, *E. validus*, *Eucommidites*, *Gnetaceaepollenites*. Angiosperm (dicotyledon): *Retitricolpites vulgaris*

Eocene

Megafossils

[88, well core drilled in the Maracaibo Basin, formation?, Eocene]

Angiosperm (monocotyledon): Palmae (rays). Angiosperms (dicotyledons): *Canna* (Cannaceae) or *Heliconia* (Heliconiaceae), *Combretum* cf. *petraflumensis* (Combretaceae), *Inga eolaurina* (Leguminosae), *Nectandra* cf. *antillanafolia* (Lauraceae), *Terminalia* cf. *phaeocarpoides* (Combretaceae)

[89, Santa Barbara–Los Barrosos, district of Sucre, state of Zulia, formation?, Eocene]

Angiosperms (dicotyledons): *Apocynophyllum* cf. *texensis* (Apocynaceae), *Burserites fayettensis* (Burseraceae), *Cedrela jacksoniana* (Meliaceae), *Chrysophyllum preoliviforme* (Sapotaceae), *Ficus americanafolia* (Moraceae)

Microfossils

[91, 71 core samples, 3 wells, Lake Maracaibo Basin area, Misoa Formation, middle Eocene]

Algae: *Chomotriletes*, *Micrast*[*h*]*erias*, *Operculodinium*. Ferns and allied groups: *Polypodiisporites*. Angiosperms (monocotyledons): *Mauritidites* (Palmae, *Mauritia*), *Spinozonocolpites* (Palmae, *Nypa*). Angiosperms (dicotyledons): *Bombacidites bellus*, *B. soleaformis* (Bombacaceae), *Echitriporites trianguliformis*, *Psilaperiporites* (chenoam), *Psilatricolporites crassus* (Pelliceriaceae, *Pelliceria*), *P. operculatus* (Euphorbiaceae, *Alchornea*), *Retibrevitricolpites triangulatus* (plant of the mangrove habitat), *Retitricolporites irregularis* (Euphorbiaceae, *Amanoa*), *Retitricolpites magnus*. Incertae sedis: *Peltandripites*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

[92, well core, state of Falcón, Jarillal Formation, late middle Eocene]

Angiosperm (dicotyledon): *Janmulleripollis pentaradiatus*

Guianas

Late Jurassic–Early Cretaceous

Microfossils

[93, North Rupununi Savannas, Takutu Formation]

Ferns and allied groups: *Converrucosisporites proxigranulatus*, *Cyathidites australis*, *C. minor*, *Deltoidospora nana*, *Densoisporites microrugulatus*, *Klukisporites elongatus* (= *Ischyosporites pseudoreticulatus*), *Laevigatosporites gracilis*, *Matonisporites* cf. *dorogensis*, *M. equiexinus*, *M. guianensis*, *Peromonolites fragilis*, *Pilosisporites trichopapillosus*, *Psilatriletes circumundulatus*, *Rotverrusporites rupununiensis*, *Undulatisporites takutuensis*, *U. undulapolis*, *Vitreisporites pallidus*. Gymnosperms: cf. *Abietineaepollenites*, *Araucariacites australis*, *A. guianensis*, *Cerebropollenites mesozoicus*, *Classopollis* cf. *torosus*, *Cycadopites* cf. *fragilis* (cf. *Monosulcites minimus*), *Ephedripites*, *Eucommiidites* cf. *minor*, *E. troedssonii*, *Exesipollenites tumulus*, *Inaperturopollenites giganteus*. Angiosperm (dicotyledon): *Tricolporopollenites distinctus*

[94, NE Guyana, coastal and bauxite belt, well and mine samples, Mackenzie and Montgomery formations, Late Cretaceous (Maastrichtian) and Paleogene (other zones Paleocene to Oligo–Miocene)]

Types of the Maastrichtian zones (A, B1): Ferns and allied groups: *Foveotriletes margaritae*. Angiosperms: *Echimonocolpites franciscoi* (Palmae, *Mauritia*), *Psilamonocolpites inornatus*, *P. medius*, *Psilatetradites umirensis*, *Psilatricolpites clarissimus*, *P. rubini*, *Psilatricolporites florschutzi*, *Retimonoporites tequendamae*, *Retitricolpites letitiae*, *R. microreticulatus*, *R. reticulatus*, *Retitricolporites florschützi*, *R. reticulatus*. **Types of the Paleocene zone** (B2): Angiosperms: *Clavatricolporites leticiae*, *Echimonocolpites franciscoi* (Palmae), *Echitriporites guianensis*, *Foveostephanocolpites perfectus*, *Gemmastephanocolpites asteroformis*, *Gemmatricolporites divaricatus*, *Polyplicadites vanegensis*, *Proxapertites operculatus*, *Psilamonocolpites inornatus*, *P. medius*, *Retidiporites botulus*, *R. magdalenensis*, *Retimonocolpites proxaperturoides*, *Retistephanocolpites angeli*, *R.* cf. *guaduensis*, *Retitricolpites analemae*, *R. cecryphalium*, *R. kwakwaniensis*, *Retitricolporites annaeoides*, *R. hispidus*, *Retitriporites retibolus*, *Scabratriporites suescae*, *Stephanocolporites ambigens*, *Syncolporites lisamae*, *Verrusyncolporites lisamae*. **Types of the Eocene zones** (C, D; mainly lower Eocene): Angiosperms: *Clavastephanocolpites crotonoides*, *Clavitricolpites annemariae*, *Echistephanoporites alfonsi*, *Psiladiporites guianensis*, *Psilastephanocolpites fissilis*, *Psilatricolpites solus*, *Retitricolporites hispidus*, *R. mariposus*. **Types of the Oligo–Miocene zones** (E, F; note the increase in modern types): Gymnosperm: *Podocarpus*. Angiosperms (monocotyledons): *Echimonocolpites franciscoi* (Palmae, *Mauritia*), *Monocolpites medius* (Palmae), *Psilamonocolpites medius* (Palmae). Angiosperms (dicotyledons): Anacardiaceae, Araliaceae, *Catostemma* type (Bombacaceae), *Clavainaperturites clavatus*, *Ilex* (Aquifoliaceae), Malpighiaceae, Malvaceae, Melastomataceae (large and small types), Myrtaceae, (*Echi-*?)*Periporites akanthos*, *Psiladiporites minimus*, *Psilatricolporites crassus*, *P. operculatus* (Euphorbiaceae, *Alchornea*), *P. rotundiporus*, *P. triangularis*, *Retistephanocolporites quadriporus*, *Retitricolporites guianensis*, *R. hispidus*, *R. irregularis*, *R. squarrosus*, *Rhizophora* (Rhizophoraceae), Sapotaceae, *Verrutricolporites rotundiporus*

[95, as above (Ref. 94), Shelter Belt No. 3 Well; Paleocene]

Angiosperms (dicotyledons): *Bombacacidites annaeoides*, *Clavastephanocolporites ambigens*, *Clavatricolporites leticiae*, *Cricotriporites guianensis*, *Cristatricolpites analemae*, *Crototricolpites annemariae*, *Echistephanoporites alfonsi*, *Echitriporites guianensis*, *Foveostephanocolpites perfectus*, *F. typicus*, *Foveostephanocolporites liracostatus*, *Gemmastephanocolpites asteroformis*, *Gemmatricolpites vigdisae*, *Gemmatricolporites berbicensis*, *G. divaricatus*, *Psilastephanocolpites maia*, *Psilastephanocolporites fissilis*, *Psilatricolpites solus*, *P. undamarginis*, *Retidiporites botulus*, *Retibrevitricolpites retibolus*, *Retistephanocolpites angeli*, *Retitricolpites agricaulis*, *R. cecryphalium*, *R. kwakwanensis*, *R. retiaphelis*, *Retitricolporites costatus*, *R. mariposus*, *Striatricolporites pimulis*, *Syncolporites lisamae*, *Verrustephanoporites simplex*, *Verrutricolpites giokinae*, *V. isolatus*, *V. verrubolus*. Incertae sedis: *Curvimonocolpites inornatus*

[96, Alliance, T-20, T-21, T-18, T-17 wells, French Guiana and Suriname coastal wells (Guiana Basin), Paleocene and Eocene]

French Guiana (Paleocene): Angiosperms: *Ephedripites vanegensis* (Araceae, gymnosperm), *Foveostephanocolpites perfectus*, *Gemmatricolpites vigdisae*, *Gemmatricolporites berbicensis*, *Heterocolpites paleocenicus*, *Mauritiidites franciscoi* (Palmae, *Mauritia*), *Proxapertites cursus*, *P. operculatus*, *Psilamonocolpites medius*, *Psilastephanocolpites maia*, *Psilatricolpites solus*, *Retidiporites botulus*, *R. magdalenensis*, *Retistephanocolpites angeli*, *Retitricolpites cecryphalium*, *R. retiaphelis*, *Retitricolporites costatus*, *R. mariposus*, *Striatricolporites pimulis*, *Verrustephanoporites simplex*, *Verrutricolpites verrubolus*, *Verrutricolporites giokina*. **Suriname (Eocene):** Angiosperms (monocotyledons): Gramineae type, *Mauritidites franciscoi* (Palmae, *Mauritia*), Palmae, *Psilamonocolpites medius*. Angiosperms (dicotyledons): *Crototricolpites americanus*, *Echistephanocolpites echinatus*, *Echitriporites guianensis*, *Foveostephanocolpites typicus*, *Gemmatricolpites vigdisae*, *Heterocolpites paleocenicus*, Malpighiaceae, Myrtaceae, *Proxapertites cursus*, *P. operculatus*, *Psilatricolpites ciliatus*, *P. hirsutus*, *P. minutus*, *Psilatricolporites cereus*, *P. crassus*, *P. rotundiporus*, *P. triangularis*, *Retidiporites botulus*, *Retitricolpites circumcanaliculatus*, *R. lalongatus*, *R. retiaphelis*, *Retitricolporites elegans*, *R. guianensis*, *R. hispidus*, *R. magnus*, *Rhizophora* (Rhizophoraceae), Sapotaceae, *Scabratricolpites simpliformis*, *Striacolporites pimulis*, *Striatricolpites minor*, *S. saramacensis*, *Triatriopollenites guianensis*, *T. infernalis*, *Verrutricolpites verrubolus*, *Verrutricolporites rotundiporus*

Brazil

Cretaceous

Megafossils

[97a, Crato Formation, late Aptian]

Gymnosperms: *Welwitschiella austroamericana* (stems with attached paired leaves), *Welwitschiophyllum brasiliense* (isolated leaves), *Welwitschiostrobus murili* (axes bearing male cone); also *Isoetites*, *Equisetites*, Schizaeaceae, Cycadales, Bennettitales, *Araucariostrobus*, *Brachyphyllum*, *Lindleycladus*, Coniferales, Gnetales (Kunsmann et al., 2004); *Cratonia cotyledon* (Rydin et al., 2003). Angiosperms: *Trifurcata flabellata*, *Arapipia florifera*, *Endressiana brasiliana* (Mohr & Rydin, 2002; Mohr & Eklund, 2003; Mohr & Bernardes de Oliveira, 2004)

Microfossils

[99, Maranhão, NE Brazil, Codó Formation, Aptian]

Ferns and allied groups: *Aratrisporites ocellatus*, *Biretisporites potoniaei*, *Camarozonosporites*, *Ceratosporites*, *Cicatricosiporites brevilaesuratus*, *C. hallei*, *C. mediostriatus*, *C. microstriatus*, *C. nuni*, *C. subrotundus*, *C. venustus*, *Crybelosporites* cf. *brenneri*, *Cyathidites australis*, *C. minor*, *Deltoidospora hallii*, *D. tenuis*, *Densoisporites*, *Gemmatriletes* cf. *clavatus*, *Klukisporites scaberis*, *Leptolepidites psarosus*, *Lycopodiumsporites facetus*, *Matonisporites*, *Perotriletes pannuceus*, *Sergipea naviformis*, *S. variverrucata*, *Stereisporites psilatus*, *Todisporites major*, *Trilites*, *Tuberculatosporites*. Pollen (undifferentiated by original author, mostly gymnosperm): *Araucariacites guianensis*, *A. limbratus*, *Bennettitaepollenites minimus*, *Circulina minima*, *C. parva*, *Classopollis intrareticulatus*, *C.* cf. *torosus*, *Cycadopites nitidus*, *Equisetosporites concinnus*, *E. costaliferous*, *E. elongatus*, *E. fragilis*, *E. irregularis*, *E. minuticostatus*, *E.* cf. *procerus*, *E. strigatus*, *E. subcircularis*, *Exesipollenites tumulus*, *Gnetaceaepollenites jansonii*, *G. oreadis*, *G. retangularis*, *Inaperturopollenites*, *Monosulcites* cf. *chaloneri*, *Peltrandipites* (gymnosperm?), *Penetetrapites mollis* (gymnosperm?), *Singhia minima*, *S. montanaensis*, *Steevesipollenites cupliformis*, *S. grambasti*. Angiosperms (monocotyledons): *Liliacidites*, *Monocolpopollenites*. Angiosperms (mostly dicotyledons?): ?*Alaticolpites limai*, *Clavatipollenites*, *Psilatricolpites*, *Reticulatasporites jardinus*, *Retimonocolpites peroreticulatus*, *Stellatopollis araripensis*, *Triangulopsis* (gymnosperm?)

[100, various sites on the continental platform of eastern Brazil; Late Cretaceous and Paleogene (to Oligo–Miocene) included here]

Fungi: *Fusiformisporites polyhedricus*. Algae: *Pediastrum paleogeneites*. Spores/pollen (undifferentiated by original author). Ferns and allied groups: *Aequitriradites*, *Ariadnaesporites spinosus*, *Cicatricosisporites baculatus* (*Anemia*), *C. cristatus*, *C. dorogensis*, *C. venustus*, *Cingulatisporites verrucatus*, *Clavatriletes disparilis*, *Echitriletes muelleri*, *Gabonisporis vigourouxii*, *Klukisporites variegatus*, *Lycopodiumsporites*

Table 7.1. Plant fossils from the Cretaceous and Paleogene of South America. *(Continued)*

novomexicanum, *Magnastriatites howardi* (*Ceratopteris*), *Matonisporites*, *Perotriletes pannuceus*, *Polypodiaceoisporites potoniei*, *Schizea certa*, *Trilites*. Gymnosperms: *Araucariacites australis*, *Classopollis classoides*, *Ephedripites pentacostatus*, *E. subtilis*, *E. undulatus*, *Gnetaceaepollenites clathratus*, *G. crassipoli*, *G. diversus*, *G. similis*, *Inaperturopollenites microclavatus*, *I. simplex*, *Podocarpidites*?, *Steevesipollenites alatiformis*, *S. amphoriformis*, *S. binodosus*, *S. duplibaculum*, *S. giganteus*, *S. multilineatus*, *S. nativensis*. Angiosperms: *Alaticolpites limai*, *Anacolosidites* cf. *luteoides*, *Applanopsis dampieri*, *Aquilapollenites magnus*, *Auriculiidites reticulatus*, *Bahiaporites reticularis*, *Buttinia andreevi*, *Clatonipollenites*(?), *Crassitricolporites brasiliensis*, *Cricotriporites alamadaensis*, *C. guianensis*, *C. operculatus*, *Crototricolpites annemariae*, *Cupaniedites reticularis*, *Echiperiporites akanthos*, *E. estelae*, *Echitricolpites communis*, *E. polaris*, *Echitriporites trianguliformis*, *Elaterocolpites castelaini*, *Elateroplicites africaensis*, *Elateropollenites jardinei*, *Elaterosporites castelaini*, *E. klaszi*, *E. protensus*, *E. verrucatus*, *Fenestrites gemmatus*, *Foveotricolpites perforatus*, *Galeacornea causea*, *Hexaporotricolpites emelianovi*, *H. lamellaferus*, *H. potoniei*, *Jussitriporites* (Onagraceae), *Longapertites proxapertitoides*, *Magnaperiporites spinosus*, *Margocolporites vanwijhei* [Leguminosae, Caesalpinioideae], *Momipites africanus*, *Monocolpites*, *Monocolpopollenites spheroides*, *Monoporites annulatus* (Gramineae), *Multiareolites formosus*, *Multiporopollenites* aff. *maculosus*, *Parvisaccites*?, *Pentapsis valdiviae*, *Perfotricolpites digitatus*, *Periretipollis spinosus*, *Perisyncolporites pokornyi*, *Peromonolites peroreticulatus*, *Proteacidites dehaani*, *P. longispinosus*, *Proxapertites cursus*, *P. facetus*, *Psilaperiporites robustus*, *Psilastephanocolporites fissilis*, *Psilastephanoporites brasiliensis*, *P. stellatus*, *Psilatricolpites papilioniformis*, *Psilatricolporites crassus*, *P. maculosus*, *P. operculatus*, *P. triangularis*, *Retibrevitricolpites triangulatus*, *Reticulatasporites jardinus*, *Retitricolpites amapaensis*, *R. americana*, *Retitricolporites amazonensis*, *R. belmontensis*, *R. guianensis*, *R. irregularis*, *R. perpusillus*, *R. quadrosi*, *R. squarrosus*, *Retitriporites mirabilis*, *Reyea polymorphus*, *Scabraperiporites nativensis*, *Scollardia trapaformis*, *Sofrepites legouxae*, *Spinozonocolpites baculatus* [Palmae, *Nypa*], *S. echinatus*, *Striatricolpites catatumbus* (Leguminosae, cf. *Crudia*), *Striopollenites dubius*, *S. terasmaei*, *Syncolporites triangularis*, *Tetradites*, *Tricolpites gigantoreticulatus*, *T. synstriatus*, *T. tienabaensis*, *Tricornites elongatus*, *Trifossapollenites*, *Triporites africaensis*, *Ulmoideipites krempii*, *Verrutricolporites rotundiporus*, *Verrutriporites asymmetricus*, *Victorisporis* cf. *roberti*, *Zlivisporis blanensis*, *Zonocostites ramonae* (*Rhizophora*)

Paleocene

Megafossils

[97b, State of Pernambuco, Maria Farinha Formation, Paleocene]

Angiosperm (monocotyledon): *Nypa pernambucensis* (Palmae)

Eocene

Megafossils

[98, São Paulo Basin, Itaquaquecetuba Formation, probably late Eocene]

Angiosperm (monocotyledon): *Monstera marginata* (Araceae). Angiosperms (dicotyledons): *Aquifoliphyllum ilicioides* (Aquifoliaceae), *Byrsonima bullata* (Malpighiaceae), *Casearia serrata* (Flacourtiaceae), *Luehea divaricatiformis* (Tiliaceae), *Myrcia* cf. *rostrataformis* (Myrtaceae), *Psidium paulense* (Myrtaceae), *Rhamniphyllum casearifformis* (Rhamnaceae?), *Schizolobium inaequilaterum* (Leguminosae), *Serjania itaquaquecetubensis*, *S. lancifolia* (Sapindaceae), *Zanthoxylum glanduliferum* (Rutaceae)

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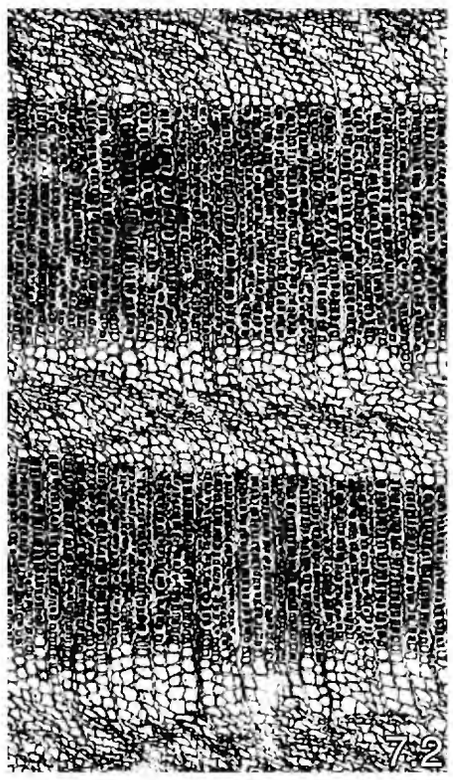
the Eocene, although its diversity and distribution suggest an earlier origin. Petrified wood with features purportedly shared among several genera of extant Rhizophoraceae has been reported from the Paleocene of Chubut Province, Argentina (Petriella, 1972). If confirmed, this would be one of the oldest occurrences of the family.

The Asteraceae is the largest and evolutionarily the most advanced family of dicotyledons, and the oldest documented fossils are from the Oligocene (but see Zavada & de Villiers, 2000, for a Paleocene–Eocene record from South Africa; Chapter 8, Asteraceae). The fossils are relatively diverse and widespread by the late Oligocene, so the family may have originated in the Eocene, although most Eocene records are suspect because of unconfirmed identifications, uncertain age of the strata, and possible contamination from the atmosphere, reworking, stratigraphic leakage, or drilling mud thinners. The oldest Asteraceae in southern South America are from the late Oligocene of Santa Cruz Province, Argentina (Barreda, 1997a). Identifications from Eocene and pre-Eocene sediments are phylogenetically and biogeographically important, and an awareness of this restrains any casual reference of early Paleogene forms to the Asteraceae.

For those studying fossil floras, another benefit to knowing the phylogenetic position of plant taxa and the proposed place and time of origin for various clades is the increased likelihood that taxa of particular significance will be recognized. For example, the group considered closest to the root of the Asteraceae tree is the Barnadesioideae. These do not have the typical "higher" Asteraceae echinate pollen, and they have no known fossil record. The Calyceraceae–Goodeniaceae is the likely complex from which the family is derived. An awareness of this increases the possibility that they will be discovered in geographically and stratigraphically important localities. This is true regardless of whether the principal goal of the study is paleoenvironmental reconstruction or lineage history, and whether it is by academic, government, or industrial researchers. The number of unpublished palynomorphs stored in geological repositories, and under-analyzed for its biological import, is many times that of all published information, and potentially it is a valuable source of paleobotanical material on specific ages and places.

Identifications and paleocommunity–paleoenvironmental lineage reconstructions are not ruled by such context information, and exceptions occasionally provide the basis for new paradigms. However, there are numerous reports in the literature that run counter to established trends. They do not reflect major geologic or environmental events; they involve taxa, communities, or environments that are implausible for a particular place and time; or they are based on barely sufficient evidence. In these cases, stating that the data are recognized as unusual and particularly significant is reassuring. These reports require special reflection when producing and close scrutiny when reading. Paleobotanical data are now being used to reconstruct biogeographic pathways, date divergences in cladograms, assess global warming, construct speciation models, and inventory the food resources of ancient cultures. This imparts new responsibilities when introducing taxa into the literature. The identifications are especially important for interpreting the already complex history of South American vegetation. The lineages reported from older deposits (Cretaceous and Paleocene) are included in Table 7.1 and in Appendix 2.1.

7.3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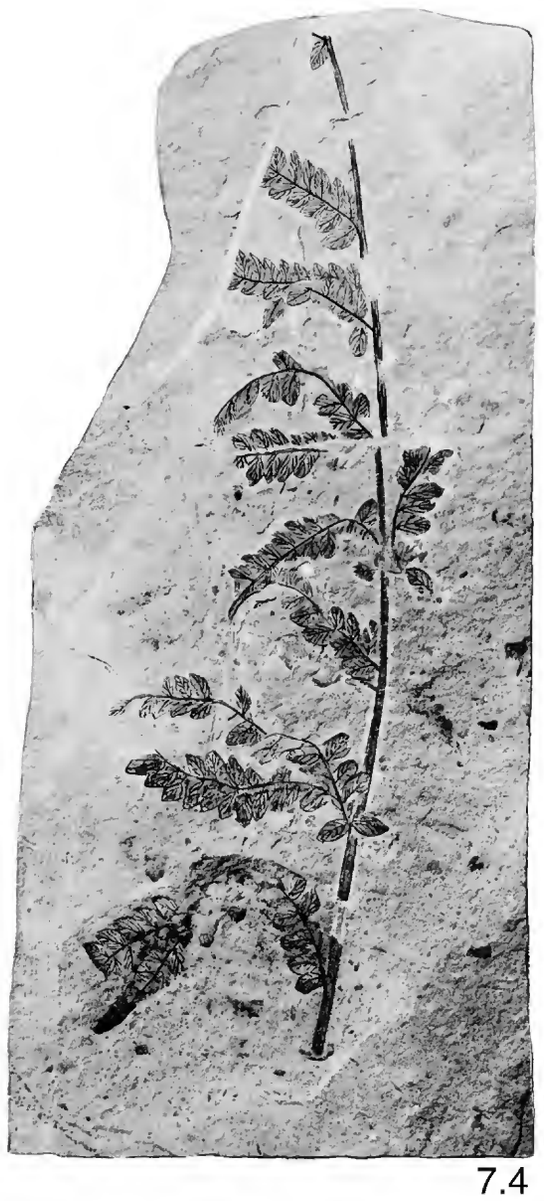
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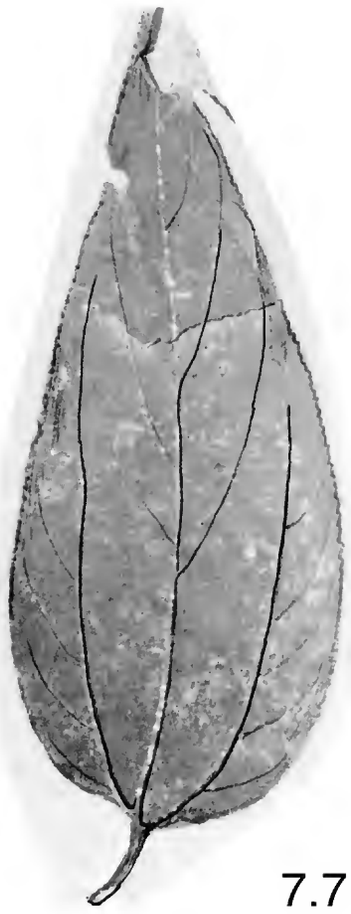
7.5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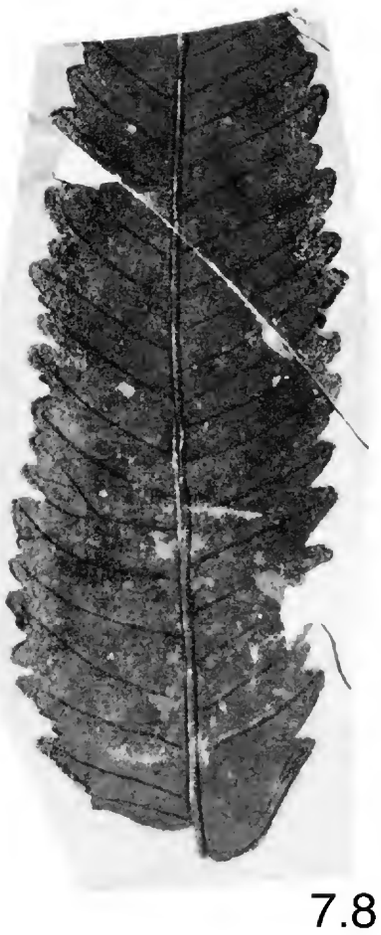
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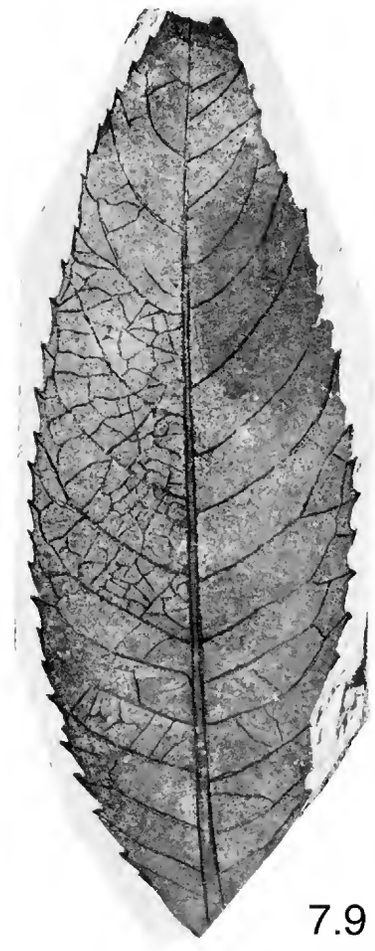
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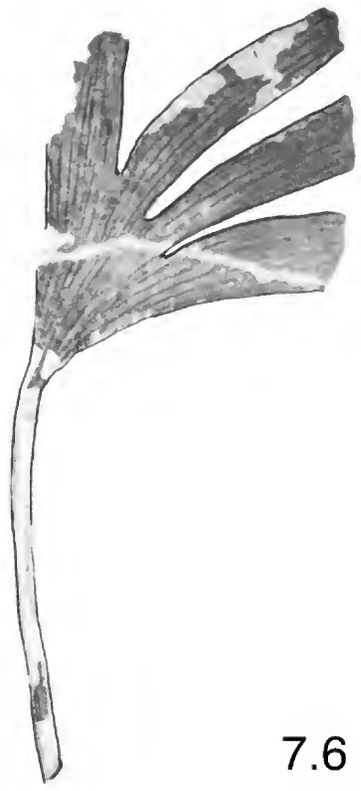
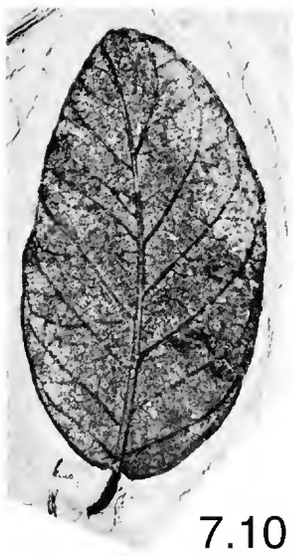

7.6

Figures 7.2–7.17. Plant megafossils from the Cretaceous and Paleogene of South America. 7.2. Cross section of wood of *Phyllocladoxylon antarcticum* showing distinct growth rings. Late Cretaceous, Chile, Nishida et al. (1992). Used with permission of the Research Institute of Evolutionary Biology, Tokyo, Japan. 7.3. *Podocarpus inopinatus*. Late Cretaceous, Chile, Menéndez (1972b). Used with permission of La Asociación Paleontológica Argentina, Buenos Aires. 7.4–7.16. Early Eocene Río Pichileu flora (Ventana Formation), Berry (1938), courtesy of Geological Society of America: 7.4. *Goniopteris patagoniana*. 7.5. *Araucaria pichileufensis*. 7.6. *Ginkgo patagonica*. 7.7. *Banara prehernandiensis*. 7.8. *Cupania grosse-serrata*. 7.9. *Cupania latifolioides*. 7.10. *Ficus patagonica*. 7.11. *Goeppertia ovalifolia*. 7.12. *Myrica mira*. 7.13. *Nectandra prolifica*. 7.14. *Ouratea firmifolia*. 7.15. *Paullinia prerufescens*. 7.16. *Symplocos commutatifolia*. 7.17. *Malvacarpus octoloculus*, Berry (1929a). (*Continued on next page.*)



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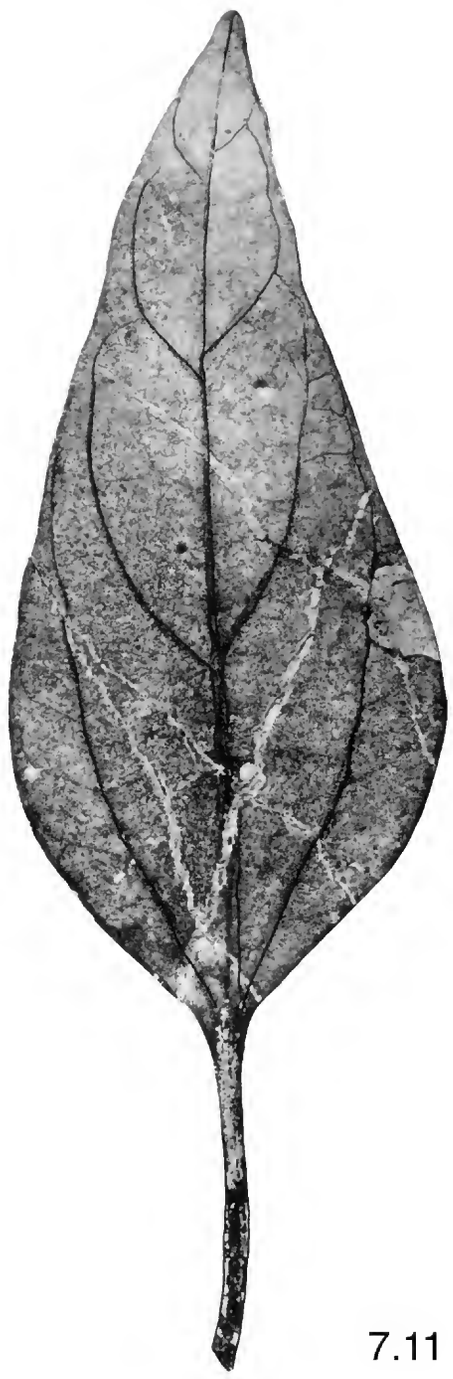

7.11

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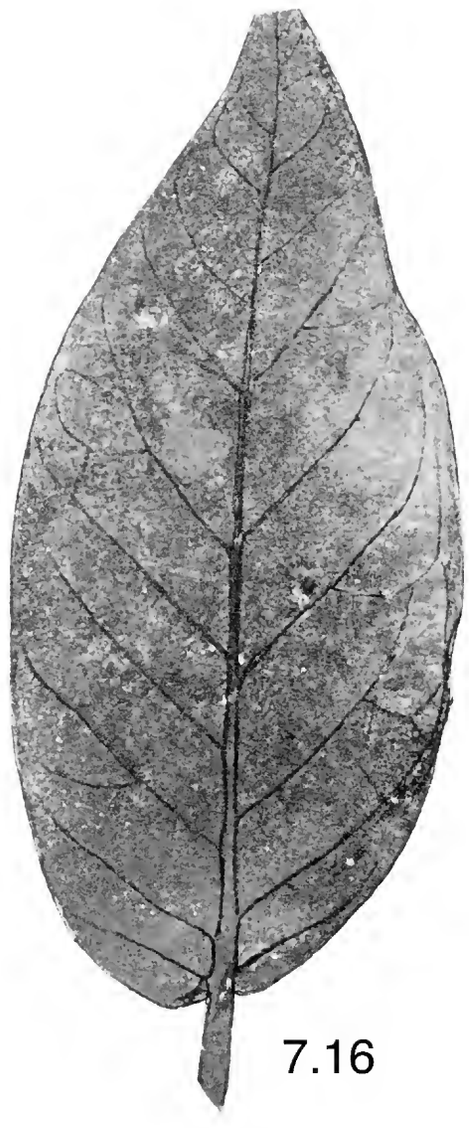


7.16

7.14

7.17

CRETACEOUS THROUGH PALEOGENE (= PALEOCENE, EOCENE, OLIGOCENE), 144–23.8 MA

Argentina and Chile (Figs. 7.2–7.54)

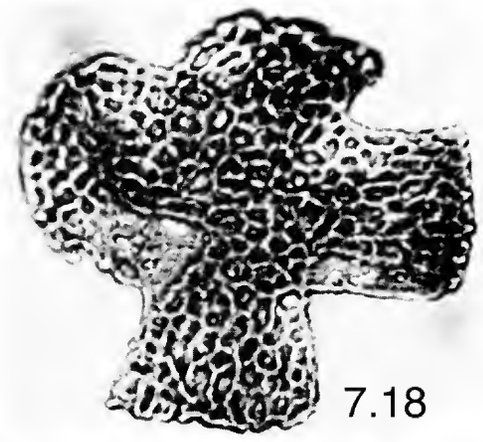
This summary of the Cretaceous and Paleogene vegetation of South America begins with Argentina because the country has the most complete sequence of published floras of that age on the continent. With this perspective, a better view is gained of the history of areas where the data are less extensive. The first paleobotanical studies in Argentina were made by F. Kurtz in the late 1800s (Kurtz, 1899, 1921). The specimens are preserved at Córdoba University, and a collection of his works was published posthumously in 1921. Joaquin Frenguelli (1883–1958) began assembling another important collection at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, and the museum continues as an important center for paleontological research. There are large collections and active programs at the Museo Paleontológico Egidio Feruglio in Trelew (Chubut Province), Universidad de Buenos Aires, Universidad Nacional y Museo de La Plata, and at several other institutes and universities (Archangelsky, 1970, 2005; Archangelsky et al., 2000). In adjacent Chile, early studies were made by Engelhardt (1895). He assigned modern generic names to Paleogene fossils familiar from Northern Hemisphere paleofloras, and later investigators such as Berry (1922a) added to them. The list now includes records that seem implausible for the Cretaceous and Paleogene of southern South America. This has left a legacy still confronted by students of tropical paleobotany, phylogeny, and biogeography, which will eventually have to be rectified through paleomonographic studies of the individual taxa. A brief bibliography of Chilean paleobotanical papers is provided by Tanai and Nishida (1981).

An Early Cretaceous flora is preserved in the Springhill Formation in the Magallanes Basin of southern Argentina and Chile (Baldoni & Archangelsky, 1983; Baldoni & Taylor, 1983; Villar de Seoane, 2001; Tables 7.1, 7.3). The megafossils consist of cuticle fragments and leaf remains of the gymnosperm *Brachyphyllum*, and *Ptilophyllum* and *Otozamites* (Bennettitales). The latter is known from the Late Jurassic–Early Cretaceous of the Antarctic Peninsula (Halle, 1913) to the Middle Jurassic of Oaxaca, Mexico (Person & Delevoryas, 1982). The microfossils also reflect a flora dominated by gymnosperms (saccate grains 30%–50%; non-saccate *Classopollis* types 15%–17%), and ferns and related groups (spores 30%–43%). Barremian-age megaspores from the La Amarga Formation in Neuquén Province add dispersed spores of *Isoetes* and *Selaginella* to the inventory (Gamerro, 1975; Prámparo & Volkheimer, 2002). Another study of plant microfossils in well cores through various Lower Cretaceous formations, primarily for purposes of stratigraphic correlation and zonation (Archangelsky et al., 1983, 1984), further documents the widespread occurrence of pteridophyte spores and gymnosperm pollen, with angiosperms (*Clavatipollenites*) first appearing in the Aptian.

An extensive fossil flora is known from the Baqueró Group of central Santa Cruz Province, Patagonia (Berry, 1924a; Feruglio, 1937; Archangelsky, 2003; Archangelsky & Villar de Seoane, 2004—Cycadales; Villar de Seoane, 1997—*Ginkgoites tigrensis* [Ginkgoales]; Del Fueyo & Archangelsky, 2001—*Karkenia incurva* [Ginkgoales]; Archangelsky & Villar de Seoane, 2005—Podocarpaceae). Earlier, the unit was called the Baqueró Formation, but Cladera et al. (2002) raised it to Group status with three formations—Anfiteatro de Ticó (oldest), Bajo Tigre, and Punta del Barco. It was assigned to the Barremian–Aptian (127–112 Ma) based on paleobotanical evidence, and a radiometric date confirmed an Aptian age (120 Ma). The flora was deposited at a time of intense global volcanism, including uplift of the massive Ontong–Java Plateau in the southwest Pacific Ocean, which contributed large amounts of CO_2 to the atmosphere. There are recurrent ash falls in the Baqueró Group (Archangelsky et al., 1995; Archangelsky, 2001) that likely resulted in additional environmental stress for an older pteridophyte–gymnosperm flora already contending with the diversification and radiation of the angiosperms in Aptian times.

The most extensive of the three floras is from the Anfiteatro de Ticó Formation, and it includes the ferns *Baqueroites padulae*, *Cladophlebis antarctica*, *C. tripinnata*, and *Cyathea cyathifolia*; the pteridosperms (seed ferns) *Ktalenia circularis*, *Pachypteris elegans*, *Ruflorinia papillosa*, *R. pilifera*, and *R. sierra*; the Ginkgoales *Ginkgoites tigrensis* and *Karkenia incurva*; and the conifers *Alkastrobus peltatus* (Del Fueyo & Archangelsky, 2005), *Apterocladus lanceolatus*, *Araucarites minimus*, *Athrotaxis ungeri*, *Morenoa fertilis*, *Nothopehuen brevis*, *Squamastrobus tigrensis*, *Tarphyderma glabra*, *Tomaxellia biforme*, and *Trisacocladus tigrensis*. It has all of the Bennettitales (Menéndez, 1966a), and most of the Cycadales (85%) and Ginkgoales (75%). A few fragmentary and poorly preserved angiosperm leaves are present (Romero & Archangelsky, 1986; Passalia et al., 2003; *Nymphaea*-type leaf) and, together with those from the late Early Cretaceous Kachaike Formation, Santa Cruz Province, Patagonia (*Kachaikenia compuesta*, *Thorphyllum patagonica*, *Rogersia australis*; Cunéo & Gandolfo, 2005), and the Aptian–Albian Crato Formation of Brazil (see later section), these are the oldest angiosperm fossils in South America. The upper Punta del Barco flora is less diverse, probably because of environmental stress, competition, and/or taphonomy (preservation factors). The Early Cretaceous floras of Argentina show the initial step in the modernization of the vegetation with a fern-gymnosperm–dominated vegetation being supplanted in many areas by an expanding and diversifying angiosperm component.

The Middle Cretaceous setting in central Patagonia consisted of basins with a multichannelled and frequently flooded fluvial system of levees, ponds, and poorly drained backswamps (Archangelsky et al., 1994). One of these is the San Jorge Basin (Figs. 7.55–7.57), well known geologically as the principal source of Argentina's hydrocarbon reserves. A spore and pollen flora recovered from the Caleta Olivia Member of the Cañadón Seco Formation within the Chubut Group (Fig. 7.56) consists of 19 types of fern spores, seven types of gymnosperm pollen, and 11 types of angiosperm pollen (Table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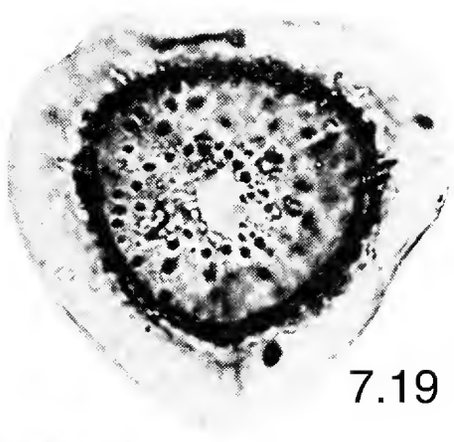
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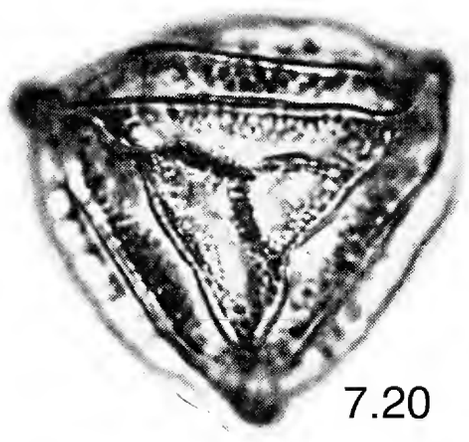
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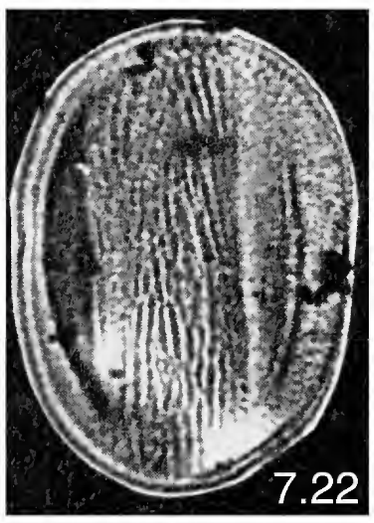
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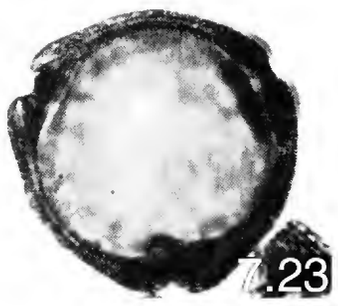
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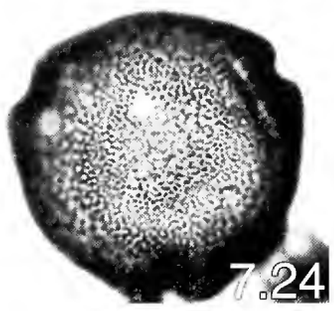
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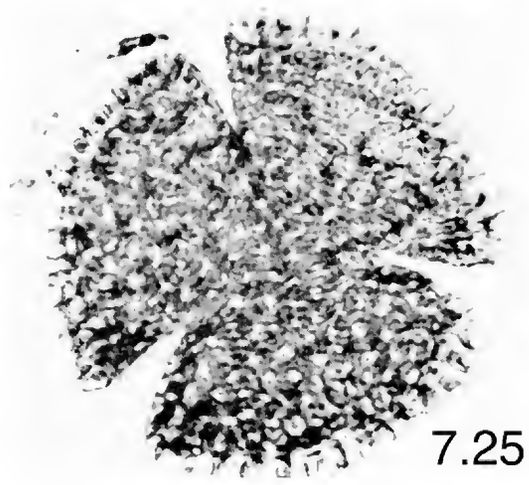
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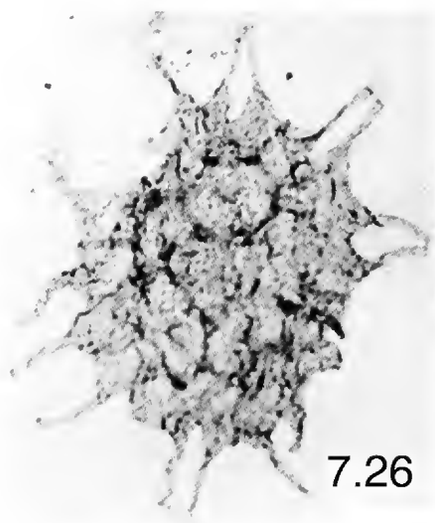
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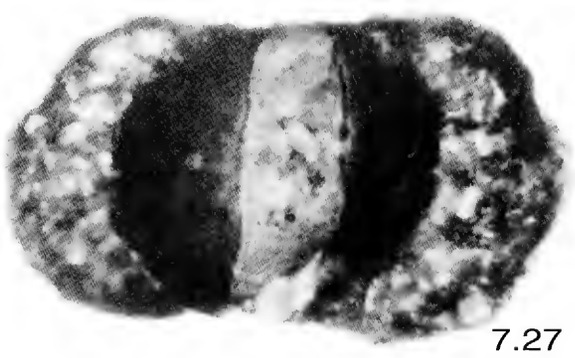
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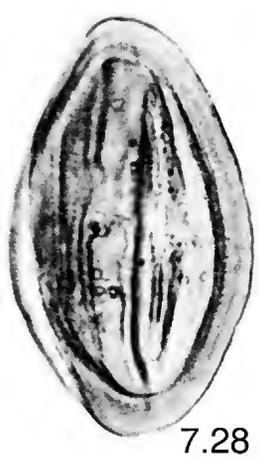
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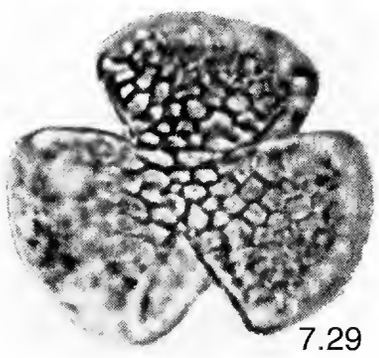
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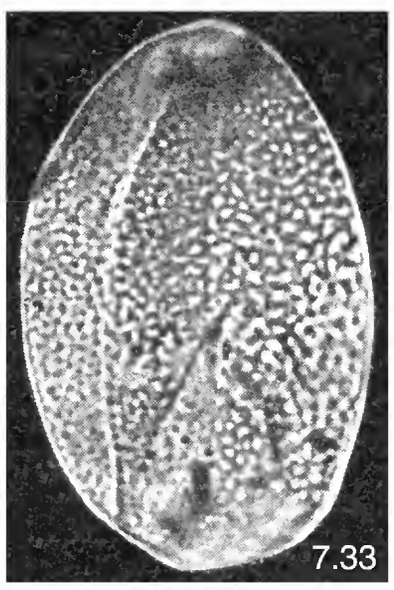
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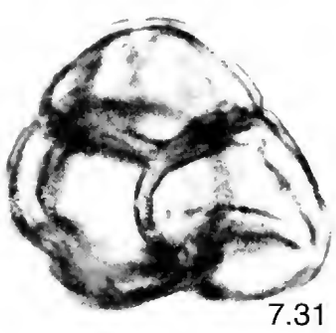
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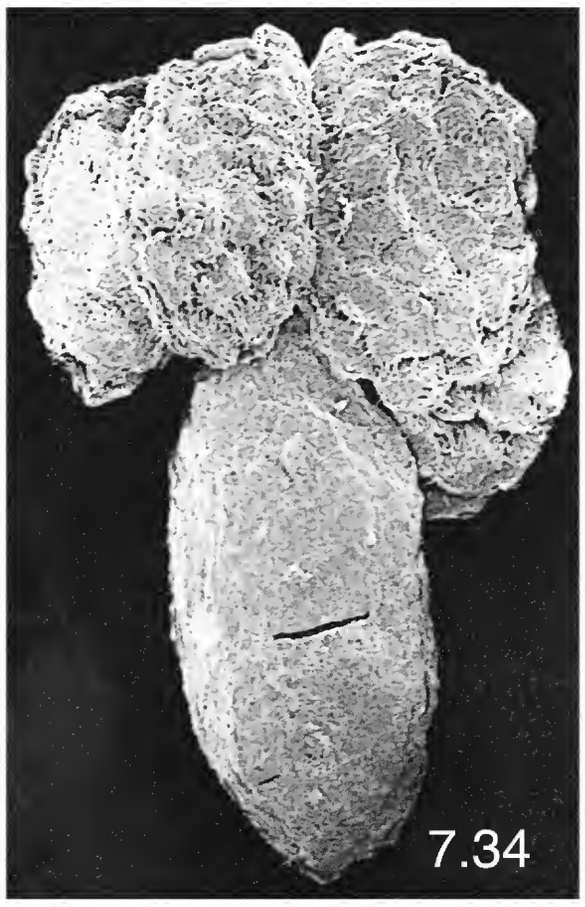
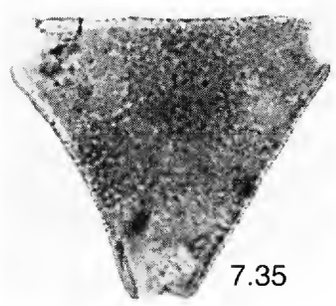
Figures 7.18–7.33. Plant microfossils from the Cretaceous and Paleogene of South America. 7.18. *Tetracolpites*. Early Cretaceous, Colombia, Pons (1988). Used with permission of Publications Scientifiques du Muséum National d'Histoire Naturelle, Paris, and Denise Pons. 7.19. *Aequitriradites spinulosus*. Cretaceous (Aptian), Argentina, Archangelsky and Gamerro (1965 et seq.). 7.20. *Cicatricosisporites baqueroensis*. Cretaceous (Aptian), Argentina, Archangelsky and Gamerro (1965 et seq.). 7.21. *Araucariacites*. 7.22. *Classopollis*. Early Cretaceous–Paleocene, Argentina, Archangelsky and Romero (1974). 7.19–7.22 used with permission of Asociación Paleontológica Argentina, Buenos Aires. 7.23 (equatorial view) and 7.24 (surface view), *Psilatricolporites crassus*. Late Cretaceous–Paleogene, Guyana, van der Hammen and Wijmstra (1964). 7.25. *Crototricolpites annemariae*. Paleocene, Guyana, Leidelmeyer (1966). 7.23–7.25 used with permission of Leidse Geologische Mededelingen, Leiden, The Netherlands. 7.26. *Pediastrum*. 7.27. *Podocarpidites*. Paleocene–Eocene, Bolivia–Chile, Horton et al. (2001). 7.28. *Psilatricolporites*. ?Maastrichtian–Paleocene, Argentina, Ruiz and Quattrocchio (1997b); used with permission of Revista Española de Micropaleontología (Geological Survey of Spain), Madrid. 7.29. *Tricolpites retielegans*. Maastrichtian–Paleocene, Argentina, Freile (1972); used with permission of the Museo de La Plata, Universidad Nacional de La Plata, Buenos Aires. 7.30. *Ephedripites*. Paleocene, Argentina, Quattrocchio and Volkheimer (1990); used with permission of Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, http://www.schweizerbart.de. 7.31. *Ericipites scabratus*. 7.32. *Retitricolporites chubutensis*, Paleocene, Argentina, Archangelsky and Zamaloa (1986). 7.33. *Liliacidites variegatus*. Paleocene, Argentina, Archangelsky (1973). 7.31–7.33 used with permission of Asociación Paleontológica Argentina, Buenos Aires.





Figures 7.34, 7.35. Plant microfossils from the Cretaceous and Paleogene of South America. 7.34. *Paleoazolla patagonica*. Late Cretaceous, Argentina, Archangelsky et al. (1999), courtesy of *American Journal of Botany*. 7.35. *Proteacidites crassus*. Paleocene, Chile, Doubinger and Chotin (1975). 7.35 used with permission of *Revista Española de Micropaleontología*, Madrid.

7.1). The differences in age between the microfossils and modern taxa preclude precise environmental reconstructions, but geologic and context evidence indicate a warm humid climate and a low-lying landscape.

General environmental conditions for the Late Cretaceous (Coniacian–Campanian) through the middle Eocene, based on independent evidence, are provided by a multi-proxy study of fossil woods from the Antarctic Peninsula across the Drake Passage from southern South America (Poole et al., 2005). The results are incorporated with other paleobotanical information in a program called Coexistence Analysis that provides the following trends in climate. The Late Cretaceous was relatively warm and wet, becoming drier and cooler in the early Paleocene, then warmer and wetter in the latest early Paleocene. During the later Eocene, climates returned to cooler and drier, beginning the trend toward icehouse conditions. If this sequence is compared with the global paleotemperature curve based on isotopic $^{16}O/^{18}O$ ratios (e.g., Fig. 6.2), the patterns are similar, supporting interpretation of the wood anatomical data and providing a useful context for reconstructing Late Cretaceous and Paleogene environments in southern South America.

Cretaceous floras have been described from Patagonia at Cerro Baguales in the Shehuen Valley in Santa Cruz Province (Berry, 1937a). They are considered Late Cretaceous, possibly Turonian, in age (Table 7.1). Floras previously described by Kurtz (1899) from the region and placed in the Cenomanian are now assigned to the Tertiary. They include such suspect identifications or implied relationships as *Abietites*, *Sequoia*, *Betulites*, *Populus*, *Quercus*, *Salix*, and *Sassafras*. The *Abietites* is *Pseudoaraucaria valentini* and the *Sequoia* is *Podocarpus inopinatus* fide Menéndez (1972b). The cycads *Brunoa santarosensis* and *Worsdellia bonettiae* are described from the Late Cretaceous of Bajo de Santa Rosa, Río Negro Province (Artabe et al., 2004).

A cautionary approach is warranted with respect to identifications in other floras from the region, as noted by Berry (1937a, pp. 11–17). An extensive and complicated study summarizing plant and animal remains from several formations and localities in southwestern Santa Cruz Province is by Hunicken (1955; Table 7.1). The floras will be revised, but in the meantime the unverified records are in the literature. The following updated age estimates are given for the formations listed in Hunicken's (1955) text and in his Table 3 (pp. 41–48; Viviana Barreda, pers. comm., 2004):

Estrados del Cerro Cazador (text) = Cerro Casador Formation (Maastrichtian)

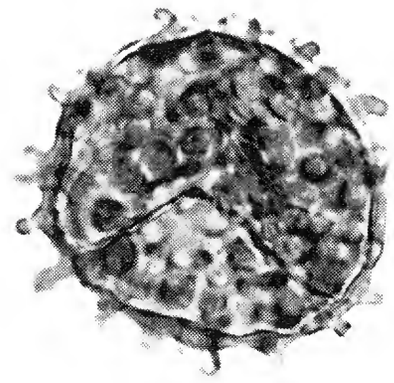
Estrados del Cerro Dorotea = Cerro Dorotea Formation (Maastrichtian–Danian, now restricted to the Danian, Malumián & Panza, 2000; table, first column, Estr. Cerro Dorotea)

Estrados de Río Turbio = Río Turbio Formation (late middle Eocene–early late Eocene [middle column, widest with several localities under "Estrados de Río Turbio"])

Estrados del Río Guillermo = Río Guillermo Formation (early Oligocene [far right column, two localities under "Estrados Río Guillermo"]).

Although many of the identifications are suspect, it is evident that by Late Cretaceous–Paleogene time, angiosperms were the prominent plants in this region of Patagonia.

Another flora is described from the Pedro Luro Formation, based on cores taken in the Colorado Basin, Buenos Aires Province. The palynomorphs are from the Danian stage (earliest Paleocene; Ruiz & Quattrocchio, 1997a, b; Quattrocchio & Ruiz, 1999; Table 7.1). The community structure and composition cannot be established based on modern analogs because of the age of the flora, and because the biological affinities of many specimens are unknown or are at the family level. One pollen type is of interest because the fossils have been reported under several generic names, and their affinities have been cited with ferns, gymnosperms, and angiosperms. The genus *Equisetosporites* was created for plant microfossils with elators (strap-like appendages twisting with changes in humidity to free the spores from the sporangium). They were thought to be related to the modern genus *Equisetum*. A study of the gymnosperm *Ephedra* pollen (Steeves & Barghoorn, 1959; see also Osborn et al., 1993) showed that compression of these elongated polysulcate grains could separate the intersulcus areas into bands somewhat resembling elators (e.g., Pares Regali et al., 1974, plate 8, fig. 5), and the genera *Ephedripites*, *Gnetaceaepollenites* (for the family Gnetaceae), and *Steevesipollenites* were created to include many of the forms previously treated as *Equisetosporites*. Lastly, the angiosperm genus *Spathiphyllum* (Araceae) also has prolate (elongated), psilate (smooth), stephanocolpate (polysulcate)-appearing pollen, it is known in the Cenozoic fossil record



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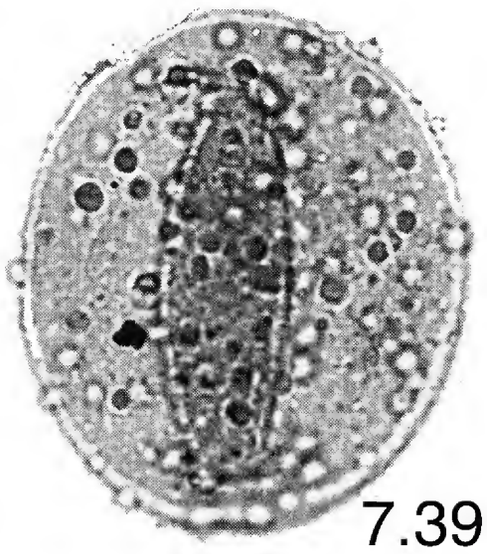

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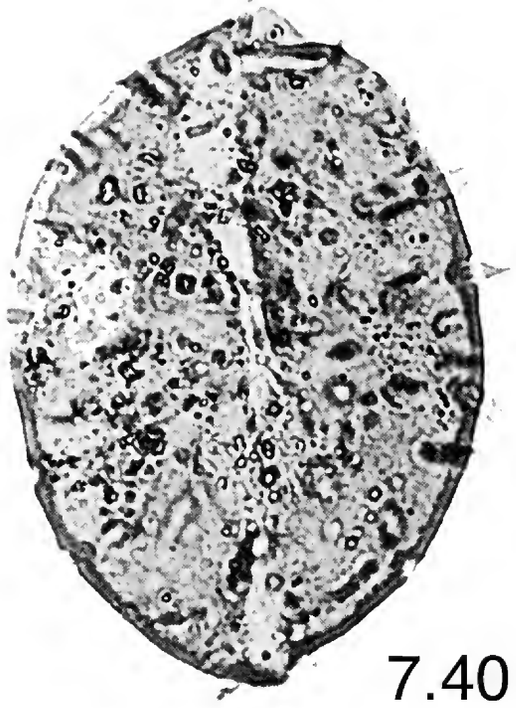

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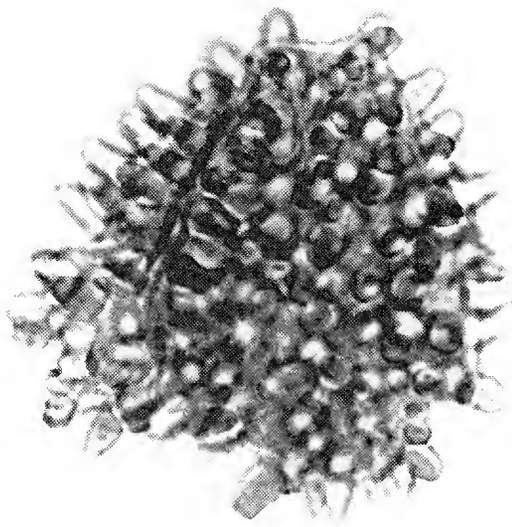

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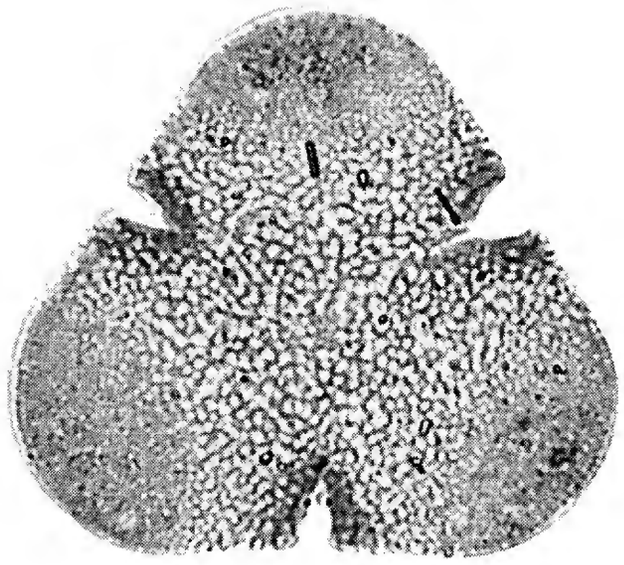

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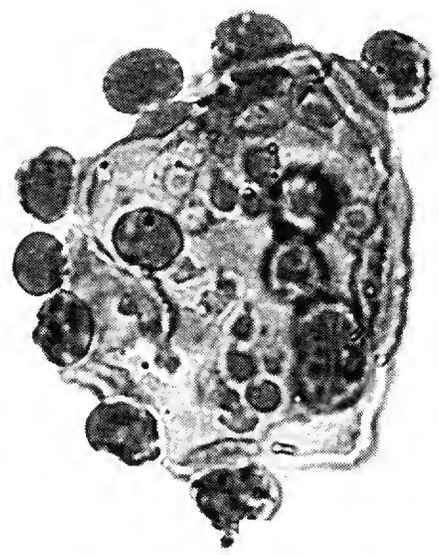

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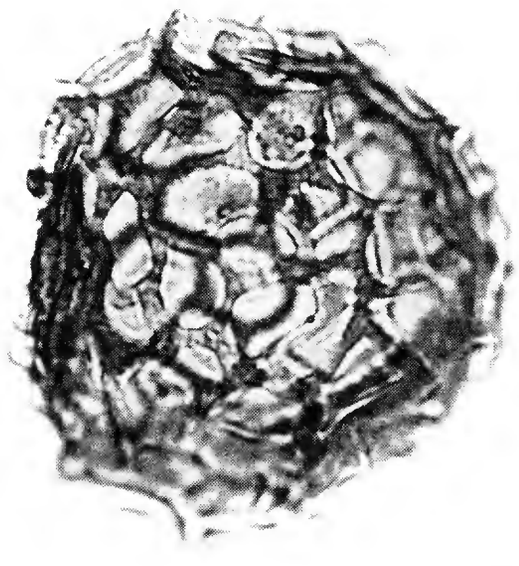

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Figures 7.36–7.45. Plant microfossils from the Cretaceous and Paleogene of South America. 7.36. *Baculatisporites*. 7.37. *Microfoveolatosporis skottsbergii*. 7.38. *Polypodiisporites* aff. *specious*. 7.39. *Gemmamonocolpites perfectus*. 7.40. *Mauritidites franciscoi*. 7.41. *Bacutriporites echinatus*. 7.42. *Bombacacidites gonzalezii*. 7.43. *Crusafontites megagemmatus*. 7.44. *Retitriporites amplireticulatus*. 7.45. *Tetracolporopollenites*. Paleogene, Colombia, Jaramillo and Dilcher (2001). 7.36–7.45 used with permission of Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, http://www.schweizerbart.de.

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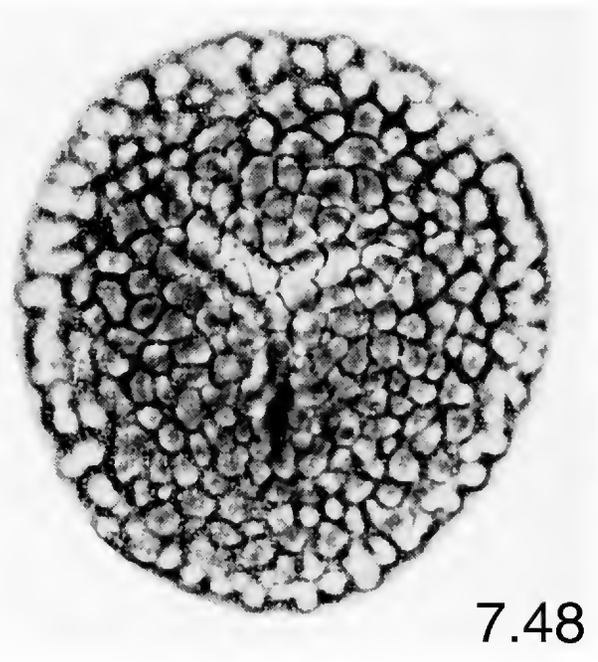
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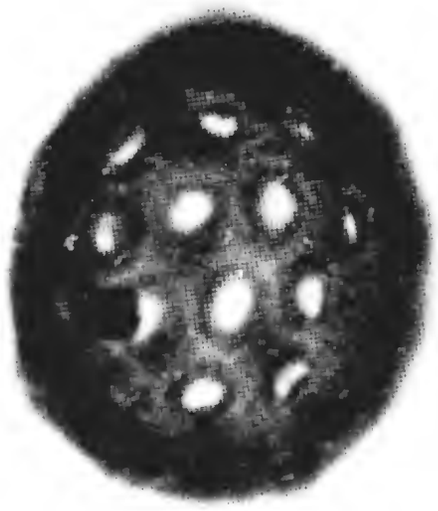
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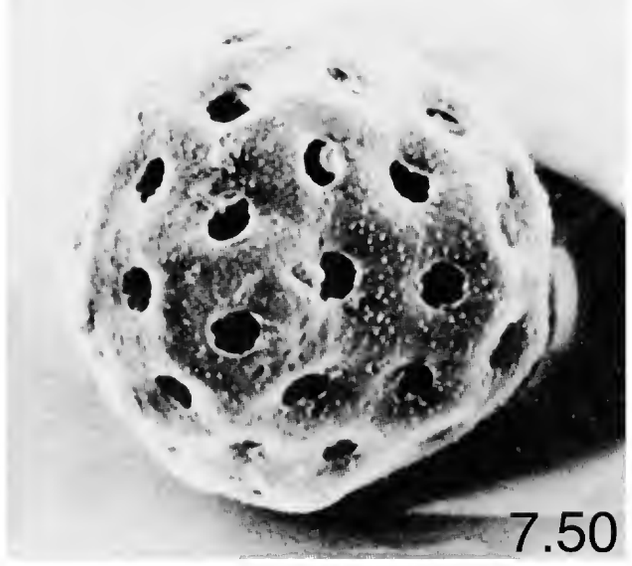
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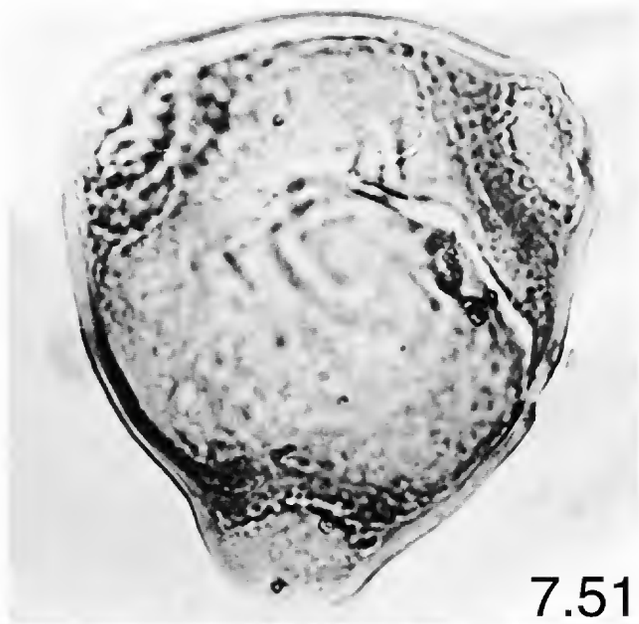
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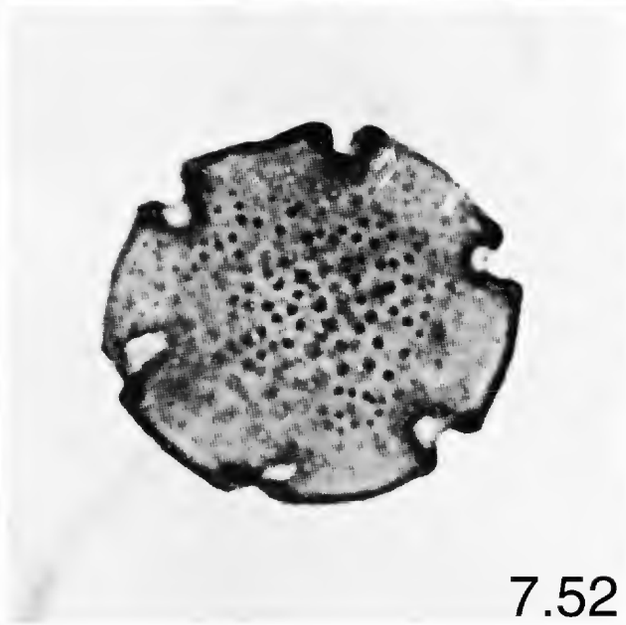
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Figures 7.46–7.54. Plant microfossils from the Cretaceous and Paleogene of South America. 7.46. *Cyathidites patagonicus*. 7.47. *Leiotriletes regularis*. 7.48. *Leptolepidites densus*, Eocene, Argentina, Archangelsky (1972). 7.46–7.48 used with permission of the Museo de La Plata, Universidad Nacional de La Plata, Buenos Aires. 7.49 (light microscopy) and 7.50 (SEM), *Chenopodipollis chenopodiaceoides*. 7.51. *Corsinipollenites atlantica*. 7.52. *Nothofagidites acromegacanthus*. 7.53. *Pseudowinterapollis couperi*. 7.54. *Striatricolporites gamerroi*, late Oligocene (?)–Miocene, Argentina, Barreda (1997d). 7.49–7.54 used with permission of Asociación Paleontológica Argentina, Buenos Aires.

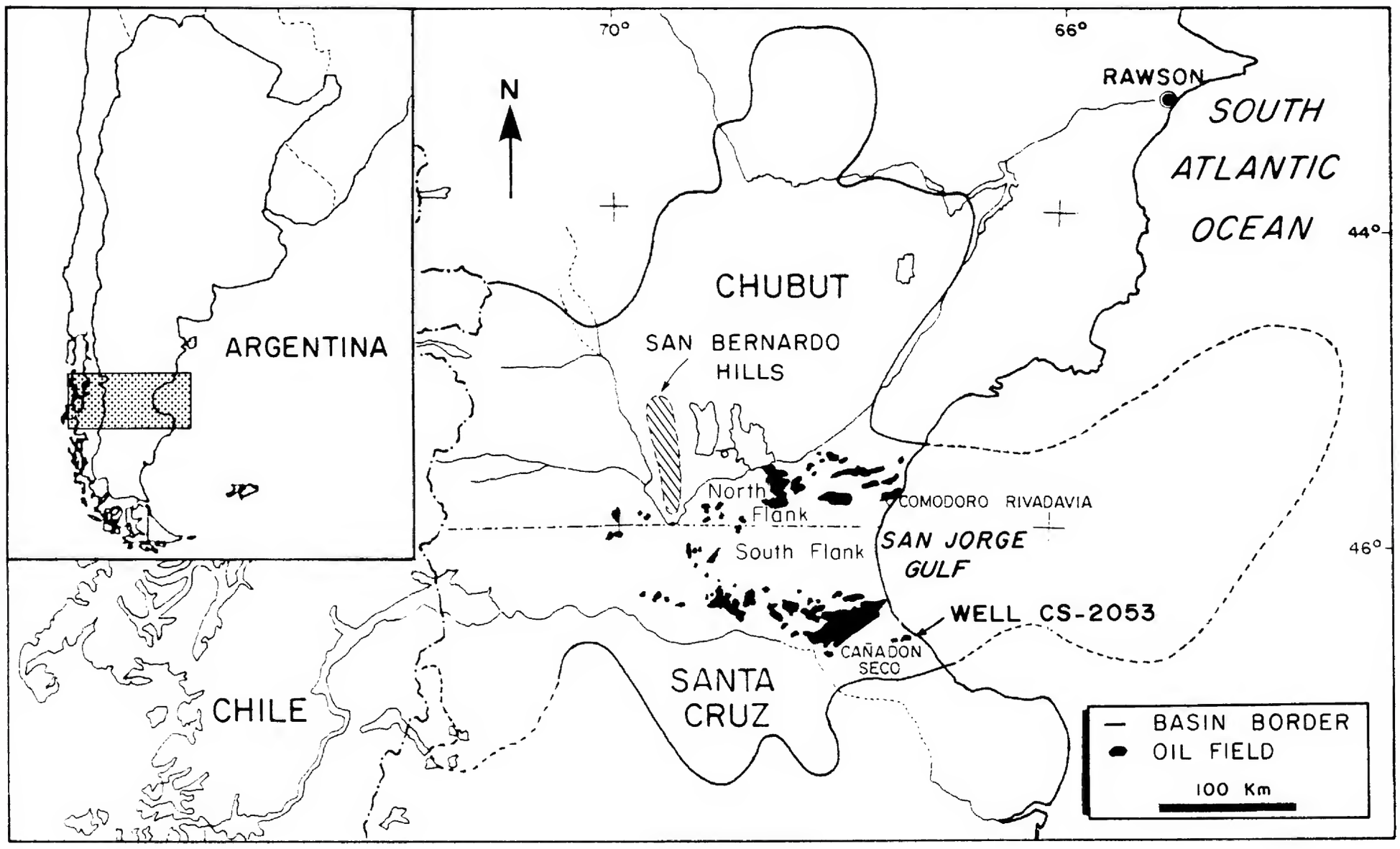


Figure 7.55. San Jorge Basin, central Patagonia, Argentina. Reprinted from Archangelsky et al. (1994), Academic Press, New York, with permission of Elsevier Science Publishers, Amsterdam.

(Table 7.1), and authors began commenting on the possible affinities of some species of *Ephedripites* (e.g., *E. vanegensis*) with *Spathiphyllum* (van der Hammen & de Mutis, 1966). The Cenozoic microfossil record of *Ephedra* and *Spathiphyllum* is now confused, and reports must be compared with specimens in modern reference collections and in surveys of *Ephedra* pollen (Steeves & Barghoorn, 1959; Osborn et al., 1993). Considering that *Ephedra* is an extreme xerophyte and that *Spathiphyllum* is a member of the moist tropical forest, the distinction is important. Until the onset of widespread, seasonally warm, dry habitats in the late Cenozoic, *Ephedra* likely existed in southern South America as a holdover from the dry component of the Cretaceous and older gymnosperm-dominated communities persisting in edaphically dry or rain shadow habitats.

Another facet of the problem involves the species concept of those describing the fossils. Pares Regali et al. (1974) use five generic names (*Elateroplicates*, *Elateropollenites*, *Ephedrites*, *Gnetaceaepollenites*, *Steevesipollenites*) and 19 species names to designate ephedroid pollen in the Late Cretaceous and Paleogene of northeastern Brazil. This is more than three times the ~6 species now found in a principal center of diversity, arid western North America. Taken at face value, this could imply the Amazon region was a virtual wasteland, or part of an extensive arid corridor between the Americas, were it not for context information and the extensive representation of fern spores and palm pollen in these sediments. Wu (1999) suggests that early representatives of *Ephedra* in the Jurassic of the People's Republic of China occupied more humid habitats because of their mat-like habit, and only later became adapted to arid environments, but modern dry-habitat, wind-blown assemblages are also found appressed to the substrate. It is also an interesting commentary on the use of molecular clocks as one method for dating lineages that Huang and Price (2003), using *rbcL* sequence data, estimate the age of extant *Ephedra* at between 8 and 32 Ma (see Ickert-Bond & Wojciechowski, 2004). Megafossils place the genus in the Early Cretaceous (Barremian, 125 Ma; Yang et al., 2006), and ephedroid pollen is known from the Permian (Wilson, 1959) onward. This emphasizes the need for a clear distinction between estimates of origin and age for molecularly defined, modern-day lineages using molecular clock evidence and estimates for the age of the genus based on fossils using the comparatively conservative characters of leaves, wood, and pollen (Rydin et al., 2004; Chapter 8).

Another important component of the Danian Pedro Luro flora is the Chenopodiaceae–Amaranthaceae complex because, as noted previously, it puts these families near the base of their stratigraphic range, and at opposite ends of the world from their oldest record in the Maastrichtian of Canada, assuming the affinities of the latter are correct and that the specimens are indigenous to the sediments. The overall aspect of the Pedro Luro assemblage suggests a warm and humid tropical forest (Quattrocchio & Ruiz, 1999).

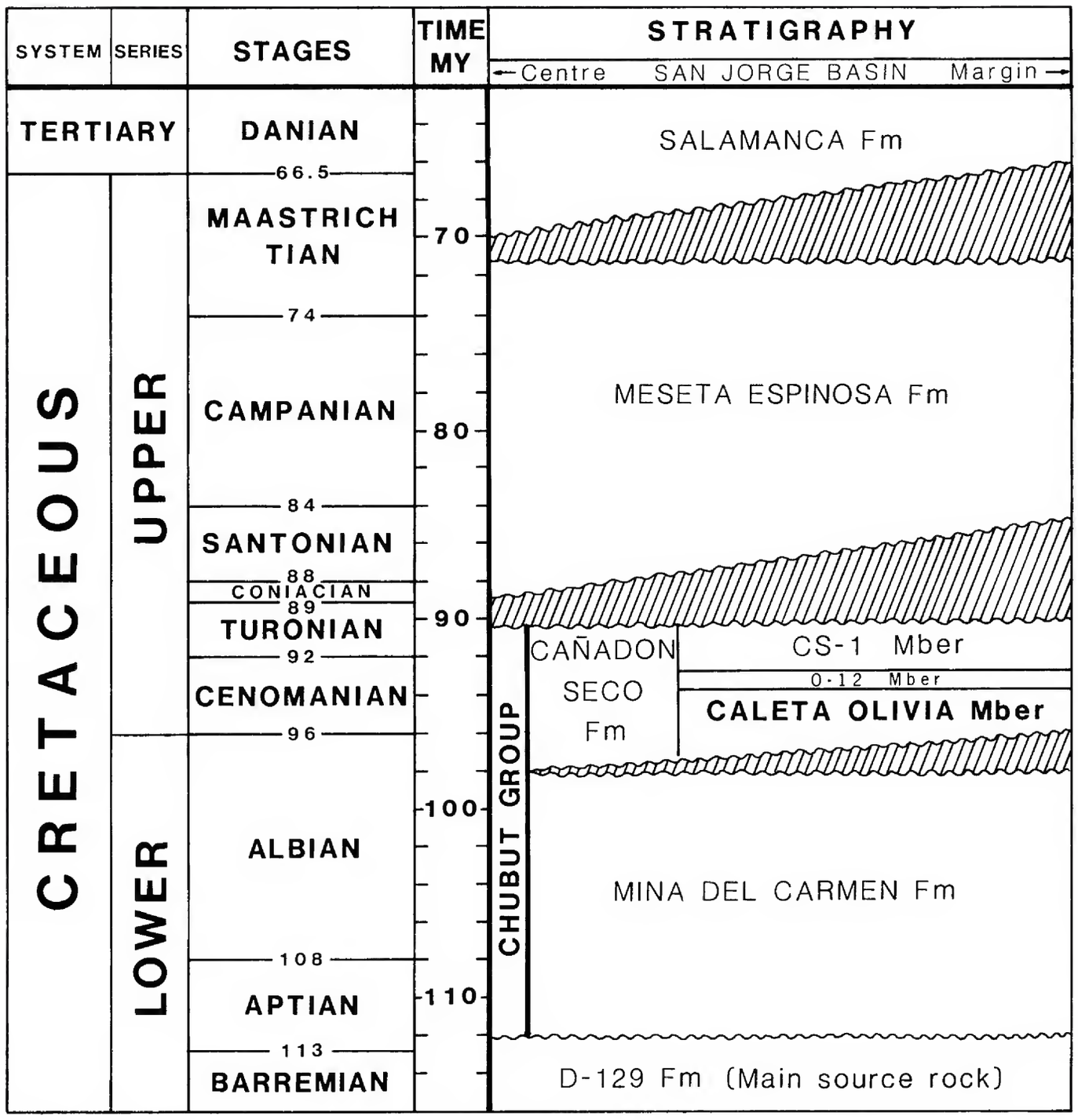


Figure 7.56. Cretaceous stratigraphy of the San Jorge Basin. Reprinted from Archangelsky et al. (1994), Academic Press, New York, with permission of Elsevier Science Publishers, Amsterdam.

Among the pteridophytes, there were holdovers from earlier Mesozoic floras such as Blechnaceae, Dicksoniaceae, Gleicheniaceae, Lophosoriaceae, Marsileaceae, Matonaceae, Osmundaceae, Pteridaceae, and Schizaeaceae (Dettmann, 1986; Dettmann & Clifford, 1992). Table 7.1 summarizes the plant fossils from Cretaceous and Paleogene sites in Argentina and Chile.

The late Mesozoic vegetation and environments of South America were influenced to a considerable extent by the interaction of the continent with other landmasses. Through about the Middle Jurassic (~180 Ma), South America was connected directly or indirectly through Africa and Antarctica with all the major lands of the Earth (Smith et al., 1994; Scotese, 2004; Fig. 7.58). Vegetation was distributed along low thermal gradients from the equatorial regions into the high northern and southern latitudes and, consequently, similar plants are found in fossil floras across vast distances of the New World during the middle and late Mesozoic (I: ch. 3, 5). For example, the gymnosperm genus *Brachyphyllum* is reported in the Cretaceous La Misión, Rosario, and Olmos floras of Mexico (Table 4.1), the Jurassic Francisco Morazán flora of Honduras (Delevoryas & Srivastava, 1981), the Cretaceous Los Ranchos flora of the Dominican Republic (Table 5.1), the Cretaceous Crato Formation of Brazil, the Cretaceous Springhill flora of Argentina and Chile, and the Baqueró Formation of Santa Cruz Province, Argentina (Traverso, 1966; Table 7.1; Fig. 1.50; see also the Early Cretaceous Ticó flora, Santa Cruz Province, Argentina; e.g., Archangelsky, 1963a–c, 1964; Menéndez, 1966b). *Pararaucaria patagonica* and *Araucaria mirabilis* are represented by cones and seedlings in the Jurassic Cerro Cuadrado Formation of Santa Cruz Province (Stockey, 1977, 1978a, b, 1982), and the lineage is also known from wood (*Araucarioxylon arizonicum*) in the Triassic Chinle Formation of the Petrified Forest of Arizona.

By the Early Cretaceous (~138 Ma), the South Atlantic Ocean was opening, and South America began separating from Africa along a rift zone in the south (Fig. 7.59). The angiosperms appeared in the late Valanginian (140.2 Ma)–Hauterivian (134.6 Ma)–early Barremian (130–125 Ma; viz., ~135 Ma) represented by small, inaperturate to monoaperturate, columellate, reticulate pollen while northern South America was still joined to Africa (see Fig. 7.60). The oldest angiosperm pollen in Patagonia is Aptian (~121 Ma). In the Late Cretaceous (Maastrichtian ~70 Ma), the position of South America in relation to the other continents is as shown in Fig. 7.61. *Nothofagus* is known from the Campanian of Antarctica and southern Australia, and from the early Maastrichtian of southern South America (Dettmann et al., 1990; Chapter 8), although *Nothofagus* forests did not develop until the middle Eocene

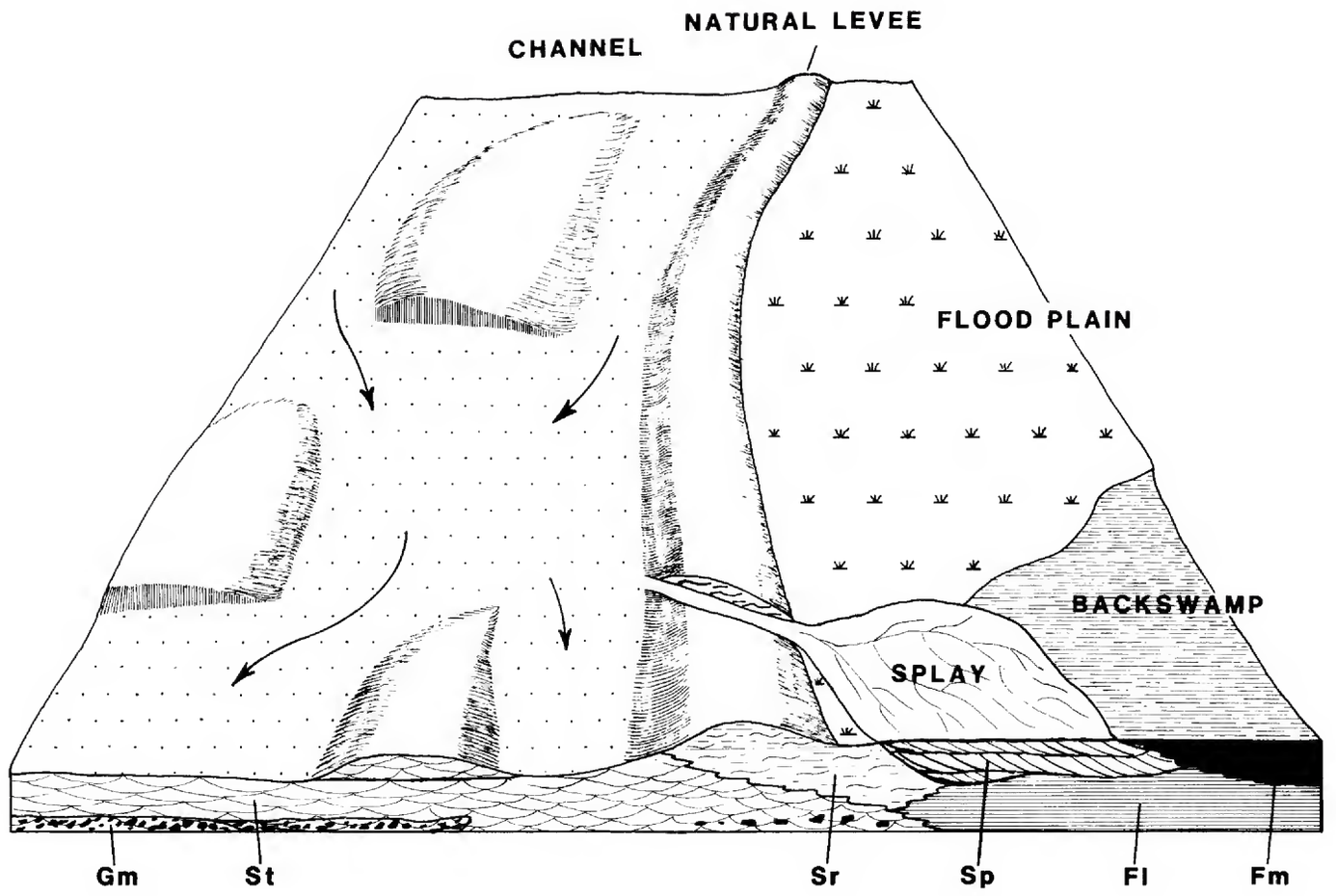


Figure 7.57. Landscape setting in the San Jorge Basin during deposition of the Caleta Olivia Member of the Cañadón Seco Formation. Reprinted from Archangelsky et al. (1994), Academic Press, New York, with permission of Elsevier Science Publishers, Amsterdam.

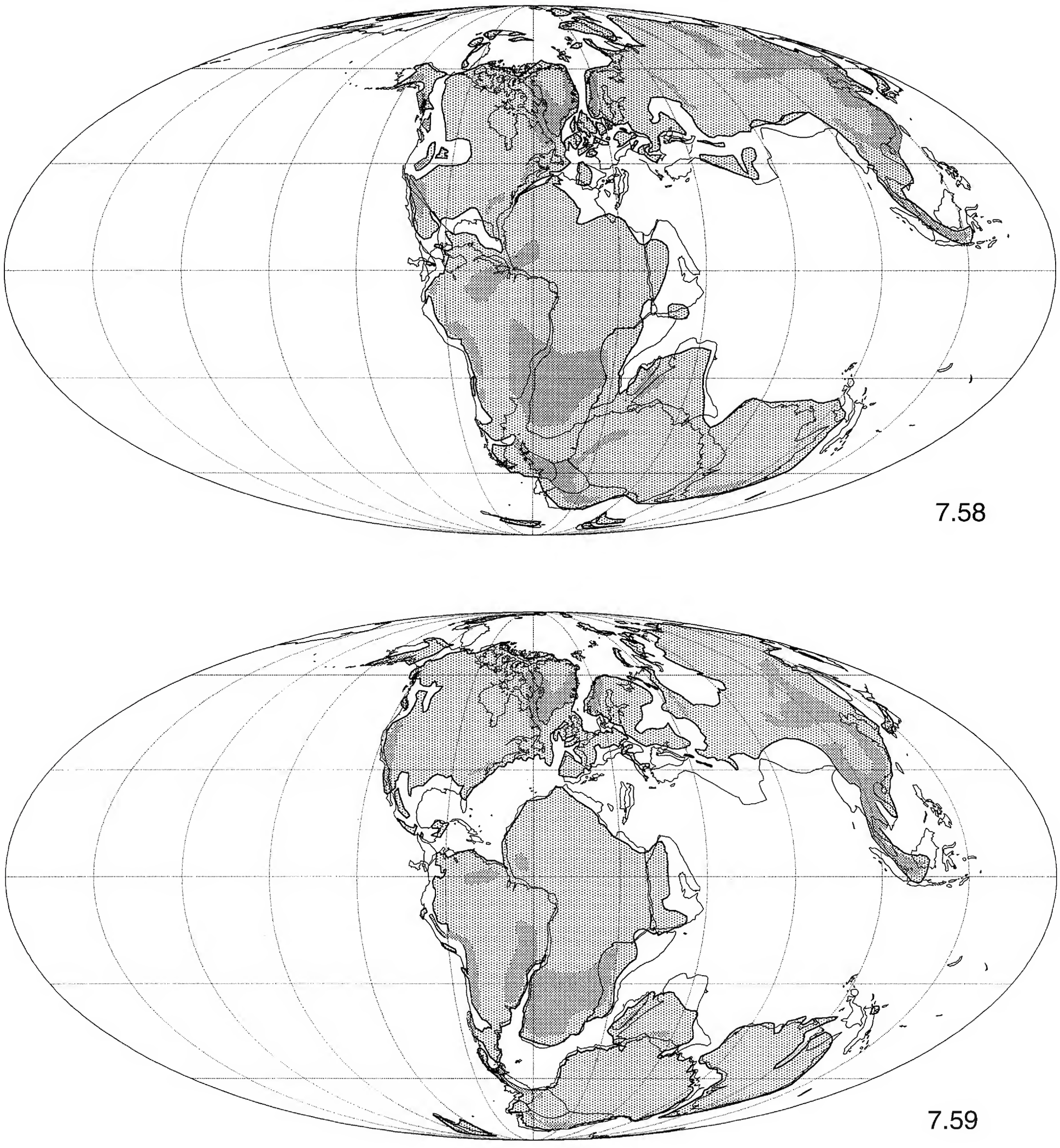
(Melendi et al., 2003; Barreda & Palazzesi, 2005). Casuarinaceae and Proteaceae are also reported from this interval. By the Paleocene, angiosperm pollen reaches 63%–79% in some assemblages in Chile (Doubinger & Chotin, 1975), consistent with global trends.

The asteroid impact on the Yucatán Peninsula at the end of the Cretaceous is marked by "an unearthly concentration of iridium" (Becker, 2002; McPhee, 1981, p. 119), and elsewhere by an increase in spores of ferns such as *Stenochlaena* (the fern spike) just above the boundary. Associating spore-increases with the impact and determining the effects on terrestrial vegetation require additional information from continuous sections across the K/T boundary, and these are rare in most parts of the world. The most devastating effect was on North American ecosystems, while the Southern Hemisphere appeared to have suffered less or not at all (Askin & Jacobson, 1996). However, evidence from the South Island of New Zealand, even farther away from the Yucatán impact site than Argentina, indicates the plant communities there may have been affected (Vajda et al., 2001). Spore and pollen profiles reveal that the area around Moody Creek Mine just prior to 65 Ma supported a swamp forest of ferns (25%), southern conifers (57% increasing to 70%), and angiosperms (14%; *Nothofagus kaitangata*; *Tricolpites lilliei*; Fig. 7.62). Just after 65 Ma, above an iridium layer, conifers decline significantly, angiosperms disappear, fungal remains become abundant (Fig. 7.63; Vajda & McLoughlin, 2004), then fern spores increase to 90%. The asteroid impact may have also affected the Late Cretaceous and early Paleocene vegetation in Argentina (Barreda et al., 2004).

Cautionary notes and opinions 3 ("Fern spikes"):

In reading the spore record it is worthwhile to recall that thick-walled fern spores can constitute nearly all the plant microfossils in a zone within a vertical sequence due to conditions of preservation and other factors unrelated to impact events. At one horizon in the early Miocene Cucaracha Formation of Panama, they represent 83% (Graham, 1988, fig. 4), and in another, they were nearly 100% of the palynomorphs. In marginally preserved assemblages in the latter stages of decomposition, fungal spores are routinely the only microfossils present. Thus, high percentages of fern and fungal spores do not, in themselves, reflect a global catastrophe; they may be the result of differential preservation and taphonomy. It is the associated geochemical evidence (viz., iridium) at a boundary and sediments with an array of plant microfossils above and below that make fern spikes attributable to an asteroid impact.

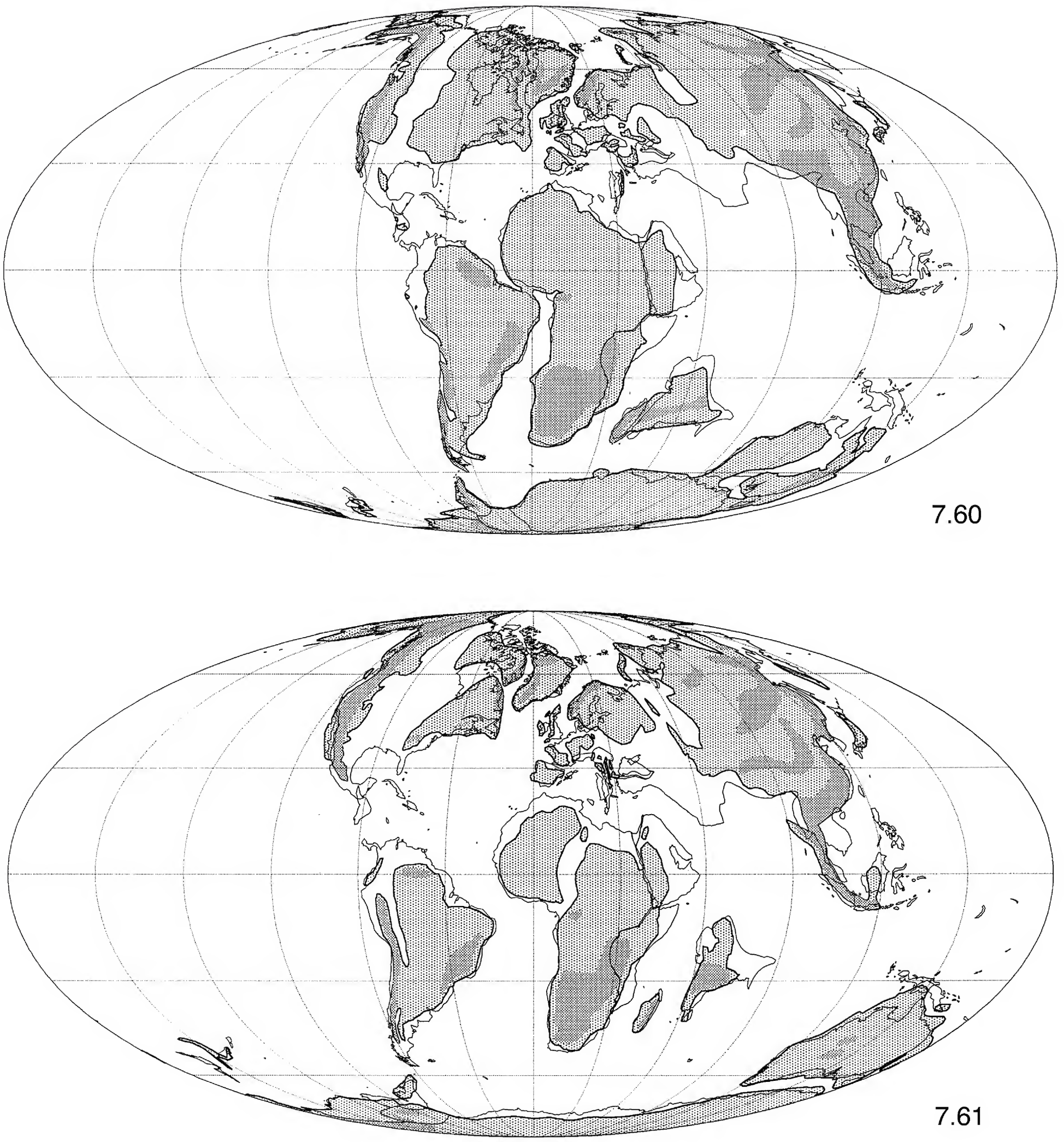
The widespread distribution of tropical to warm-temperate climates and vegetation from equatorial regions extending far into the higher northern and southern latitudes in the Late Cretaceous and Early Tertiary is well established (e.g., in Arctic floras, the Eocene London Clay flora of England, the Paleogene floras of Australia and New Zealand; Adams et al., 1990; Graham, 1994; Pagani et al., 2006; I: ch. 5; Chapter 8). Temperatures in the Arctic Ocean were ~15° C at 70 Ma and 20° C at 90 Ma (Jenkyns et al., 2004). The terrestrial climates in southern South America at this time are difficult to infer directly from fossil plants because the interval between the fossils and their nearest living relatives is great. However, the large number of ferns, palms, Annonaceae, Bombacaceae, Lauraceae, and others, and the generally large size of the leaves (megaphylls and notophylls), indicate that the conditions were warm and humid (Petriella & Archangelsky, 1975; Quattrocchio, 1978b; Quattrocchio et al., 1988, 1997; Quattrocchio & Volkheimer, 1988, 1990). Some Late Cretaceous woods from central Patagonian Chile (Nishida et al., 1992) show distinct growth rings indicating seasonality in rainfall and temperature, particularly in the inland-upland habitats (*Araucarioxylon pichasquense*, *Phyl-*



Figures 7.58, 7.59. Reconstructions of Mesozoic coastlines. 7.58. 170 Ma (Bajocian). 7.59. 138 Ma (Valanginian–Berriasian). From Smith et al. (1994). Reprinted with the permission of Cambridge University Press. See also Scotese (2004).

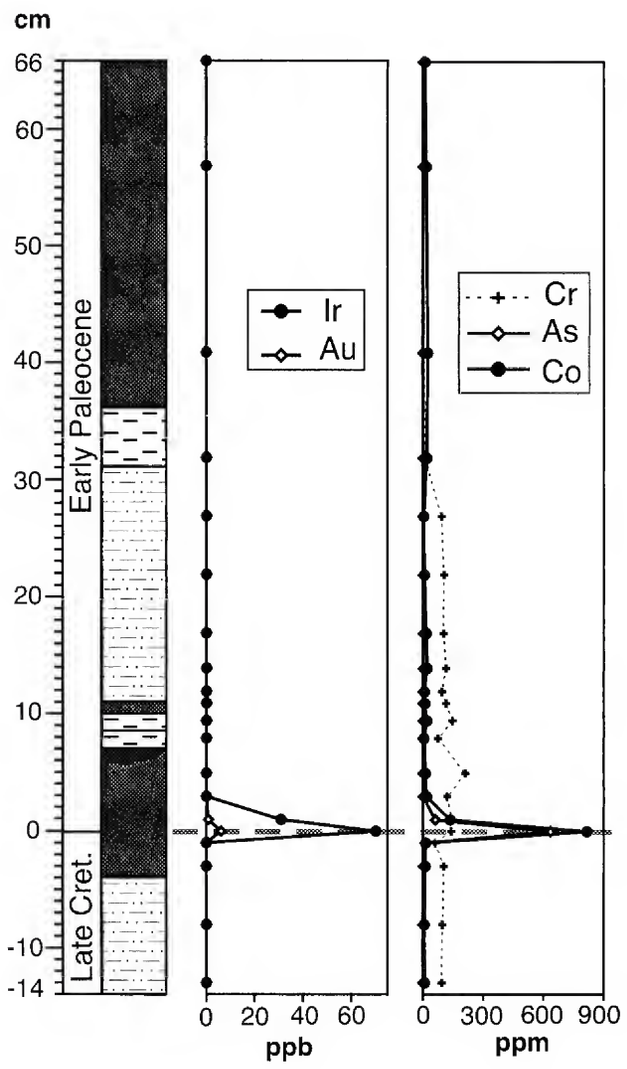
locladoxylon antarcticum; Fig. 7.2), while other woods lack growth rings (e.g., *A. kellerense*). A more quantitative estimate of the climate is afforded by leaf margin and leaf area analysis of the early Eocene Laguna del Hunco flora of Patagonia (~45°S; paleolatitude ~47°S; Wilf et al., 2003; Fig. 7.64). These analyses suggest a minimum MAT of ~18° C, with a warming of ~6° C through the section, and a winter minimum of >10° C. The absence of the temperate *Nothofagus* is further support of a mild climate. Sea surface paleotemperatures at other sites in the South Atlantic yield values of ~17° C. MAP is estimated at a minimum of ~1200 mm.

The widespread geographic affinities of southern South American vegetation evident in the Cretaceous are shown by similarities in pollen assemblages between Australasia (e.g.,



Figures 7.60, 7.61. Reconstructions of Mesozoic coastlines. 7.60. 105 Ma (Albian). 7.61. 70 Ma (Maastrichtian). From Smith et al. (1994). Reprinted with the permission of Cambridge University Press. See also Scotese (2004).

Cookson & Pike, 1954; Cookson & Cranwell, 1967; Couper, 1953, 1960) and Argentina–Chile in the Paleogene. There are microfossils in Chile attributed to the Australasian *Casuarina* (Doubringer & Chotin, 1975), megafossils identified as *Casuarina–Gymnostoma* in the Laguna del Hunco flora (Table 7.1; Zamaloa et al., 2006), and fossils of *Blechnum*, *Gleichenia*, *Hymenophyllum*, *Araucaria*, *Dacrydium*, *Microcachrys* (Podocarpaceae, one species, Tasmania), *Podocarpus*, *Gunnera*, *Laurelia*, *Tricolpites fillii* (similar to *Beauprea* [Proteaceae, ~10 species, New Caledonia]), and numerous other plant fossils widespread throughout the region. Although morphological similarity does not equate to biological identity, the plate tectonic, climatic, and paleontological record indicates that no major physical or climatic barrier existed between southern South America and Australasia



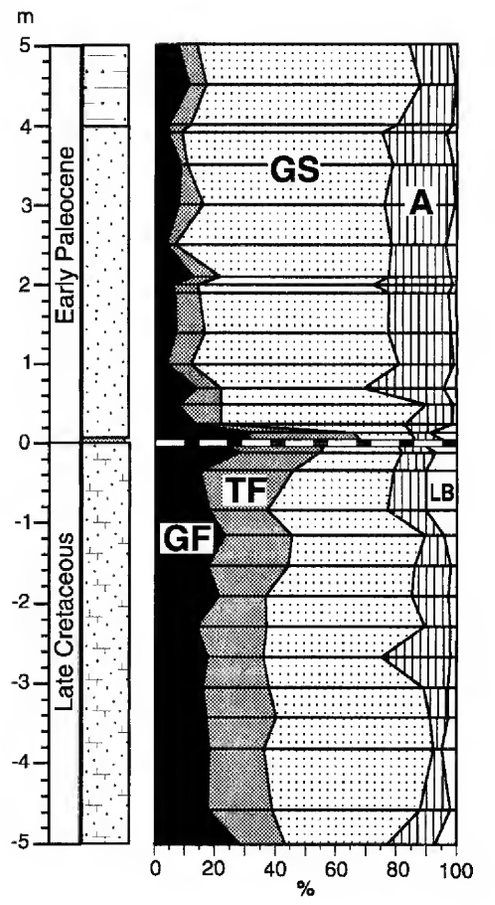


Figure 7.62. Geochemical signature (Ir, Au, Cr, As, Co; top) and abundance of main spore and pollen types (bottom) across the K/T boundary, Moody Creek Mine, New Zealand. GF = ground ferns, TF = tree ferns, GS = gymnosperms, A = angiosperms, LB = lycopods and bryophytes (including *Sphagnum*). From Vajda et al. (2001). Used with permission of *Science*, American Association for the Advancement of Science, Washington, D.C.

in the Late Cretaceous and Paleogene.

The question of a temperature decline with associated greater seasonality in rainfall toward the end of the early Eocene in southern South America is also difficult to address using the modern analog method, but palynofloras from the Salta Basin in northwestern Argentina indicate cooler temperatures beginning sometime in the early Eocene (Quattrocchio & Volkheimer, 1990). A gradual lowering of temperatures is further suggested by leaf margin analysis (Romero, 1986). In the early Eocene Lota and Coronel floras of Chile, 70% of the species have entire-margined leaves, indicating a paratropical forest (I: pp. 149–150). In the middle Eocene Río Turbio flora, the figure is 40% (subtropical rain forest), and in the late Eocene Ñirihuau flora in northwestern Patagonia it is 27% (mixed mesophytic forest). It seems clear that declining temperatures beginning in the middle Eocene were among the factors causing change in the vegetation (Barreda, 2007).

It has been noted previously that global trends in past vegetation and a wide variety of context information are useful in tracing the history of plant formations and identifying the forcing mechanisms directing that history. It also has been emphasized that this information should not preclude cautious acceptance of new interpretations that run counter to conventional wisdom. A case in point is the expectation that the mode and tempo of evolution should increase the number of species over time as the gene pool diversifies, and as the increasing complexity of the landscape provides a wider range of habitats to accommodate the novel phenotypes. In general this is true, but there is evidence for higher-than-realized species diversity in ancient times. Wilf et al. (2003, 2005) report 186 plant organs (152 leaf types) from the Laguna del Hunco flora (Refs. 25–27 in Table 7.1), radiometrically–paleomagnetically dated at 51.9 Ma, within the LPTM–EECL warm interval. The Río Pichileufú flora (47.4 Ma) is also highly diverse. According to the authors, "observed species richness exceeds that of any other Eocene leaf flora" when adjusted for sample size and that "elevated plant diversity is an ancient feature of South America" (Wilf et al., 2003). In the Paleocene Salamanca Formation (~61.7 Ma; ~4 Ma after the K/T impact) of southern Chubut Province, Patagonia, Iglesias et al. (2007) report an exceptionally rich flora with 50% more species than in comparable Paleocene floras from North America. Undoubtedly, as more such studies are made, our views on the geography of ancient biodiversity will be much improved. A similar pattern is evident in Paleocene to early Miocene palynomorphs in Colombia and Venezuela (Jaramillo et al., 2006). Among the causal factors were the vast extent of the interconnected landscape, the prevailing equable climate, and, for the southern South American biota, the distance from the K/T impact.

The Laguna del Hunco flora suggests that elevations throughout most of the region were low. The composition of the flora (palms, cycads, araucarias, podocarps) shows that no rain shadow was cast from the west (Hinojosa & Villagrán, 2005), and this is consistent with geologic evidence on the uplift history of the Southern Andes. Throughout the early Paleogene, the plant formations and associations are without close modern analogs. There is no evidence for modern communities of desert, shrubland/chaparral–woodland–savanna, grassland, páramo, or tundra. The principal community based on the identifications in Table 7.1 was a gymnosperm forest of

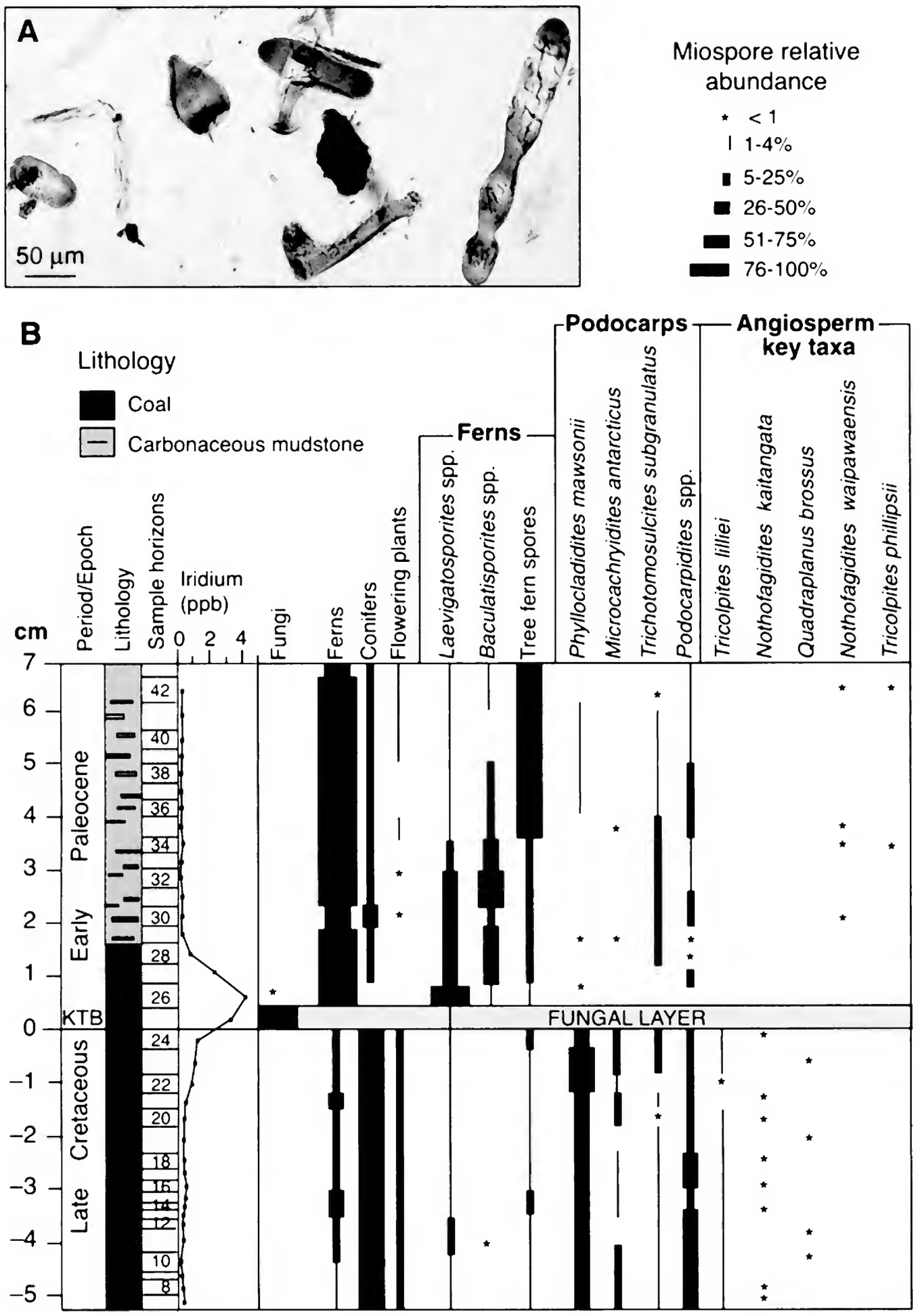


Figure 7.63. Iridium layer and fungal spore spike across the K/T boundary at Moody Creek Mine, New Zealand. From Vajda and McLoughlin (2004). Used with permission of *Science*, American Association for the Advancement of Science, Washington, D.C.

increasingly modern aspect with *Araucaria*, soon augmented by *Acmopyle* (Taxaceae, San Jorge Basin flora; presently three species in New Caledonia and Fiji), *Podocarpus* (e.g., in the Baqueró Group), and plants with *Podocarpus*-like pollen (e.g., *Podocarpidites* cf. *ellipticus* in the Springhill flora). There was an ancient version of the lowland Neotropical rain forest and lower altitudinal representatives of the lower to upper montane broadleaved forest. Included were palms (*Palmoxylon patagonium* in the La Colonia Formation), *Nothofagus* appeared near the Cretaceous–Paleocene boundary (pollen in the Maastrichtian, leaves in the Paleocene; Romero, 1986, p. 451), and modern and extinct genera of numerous tropical families are reported from the Paleocene (Table 7.1).

It is interesting to consider what plants might have occupied the mangrove habitat in the Neotropics prior to the arrival of *Rhizophora* in the middle Eocene. Pre-middle Eocene pollen occurring in the same high abundance as *Rhizophora* in coastal sediments to the north are *Brevitricolpites variabilis* and *Retibrevitricolpites triangularis* in Venezuela and Colombia (e.g., in the middle Eocene Mirador and Misoa formations), but their biological affinities are unknown and they have not been reported from southern South America. The extant mangrove *Pelliceria* (Theaceae) is known from the Eocene in the north, but it also has not been found in southern South America. The Old World mangrove palm *Nypa* (*Spinozonocolpites*) is known from the Salamanca–Bororó and Mealla formations of

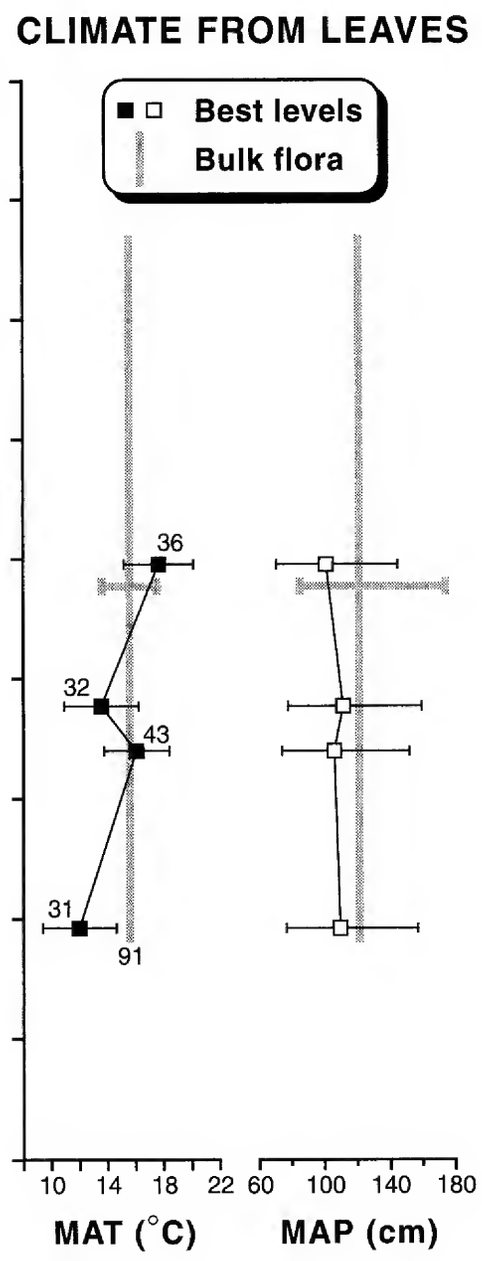


Figure 7.64. MAT and MAP estimates from leaf margin analysis of the early Eocene Laguna del Hunco flora, Patagonia, northwestern Chubut Province, Argentina. From Wilf et al. (2003). Used with permission of *Science*, American Association for the Advancement of Science, Washington, D.C.

Argentina, *Rhizophoroxylon spallettii* is reported from the Cerro Bororó Formation, and trilete spores that are similar (but cannot be referred specifically) to the mangrove fern *Acrostichum aureum* are widespread. Palms and ferns were prominent, but the composition of pre-*Rhizophora* brackish coastal communities is not well known. The present southernmost distribution of *Rhizophora mangle* in South America along the Atlantic coast is near 27°53'S, Porto Alegre, Brazil. As noted, the Rhizophoraceae affinities of Paleogene wood from Argentina is pending (Petriella, 1972).

Although beach/strand/dune, freshwater herbaceous bog/marsh/swamp, and aquatic habitats were undoubtedly present, recognition of the plant formations depends on comparisons with modern analogs and this is usually not possible for the Late Cretaceous, Paleocene, and early Eocene. Some palms may have occupied beach/strand/dune habitats, and ferns and bryophytes (poorly known in the fossil record) were likely prominent in bog/marsh/swamp communities. Among other fossils relevant to these plant formations are *Azolla* (Paso del Sapo, Pedro Luro, Malargüe, Mealla, Chenque formations), *Cyperaceaepollis* (Cyperaceae; Chenque Formation, early Miocene [Palamarczuk & Barreda, 1998; Barreda & Palamarczuk, 2000b]; early Eocene [?], no formation, Table 7.1), *Poacites* (Poaceae; Río Turbio, Ventana, San Julián, Chenque formations), *Myriophyllumpollenites* (Tunal/Mellea formations), *Pandaniidites* (Tunal Formation), *Potamogetonaceaepites* (Pachaco Formation), and *Sparganiaceaepollenites* (San Julián, Chenque formations; Aries x-1 Well, Oligo–Miocene, no formation).

The plant formations in the Danian of Argentina may be grouped into the communities shown below. If the assigned modern generic or family affinities are accepted (Combretaceae, *Ruta*, *Smilax*), they show a cline in provinces from the south (temperate, *Nothofagidites*) to the north (tropical, *Verrustephanoporites simplex*; fide Quattrocchio & Volkheimer, 2000). The plant formations are:

Freshwater herbaceous bog/marsh/swamp
- Marsh (*Pandaniidites*)
- Lake (*Myriophyllumpollenites*)

Lower to upper montane broad-leaved forest
- Subtropical forest, moist forest (*Verrustephanoporites* = *Phyllostylon*)
- Lower montane forest (Anacardiaceae [*Retitricolporites* sp. A]; Aquifoliaceae [*Gemmatricolpites subsphaericus*]; Rutaceae [*Rhoipites* sp. A])

These generalized plant communities, with early representatives that would later evolve into more distinct tropical, temperate, arid, and high-altitude plant formations, have been grouped from north to south into Neotropical, mixed, and Antarctic paleofloras (Romero, 1986). Similar formations occurred in Chile in the Late Cretaceous and Paleogene (Table 7.1; Hinojosa & Villagrán, 1997). Collectively, they may be viewed as a relatively undifferentiated Austrotropical flora (or "paleoflora mixta"; Romero, 1978) comparable to the Northern Hemisphere Boreotropical flora of similar age (I: p. 109).

Uruguay, Paraguay, Bolivia, Peru, Ecuador

There are no Late Cretaceous or Paleogene floras published for Uruguay or Paraguay. In Bolivia, palynomorphs were recovered from the Cretaceous–Paleocene Flora and Eslabón formations (Vajda-Santivanez, 1999) and the late Eocene–Oligocene Potoco Formation of the Altiplano (Horton et al., 2001; Figs. 7.26, 7.27). The overall aspect is a low to mid-elevation vegetation (Podocarpaceae, Ulmaceae, Bombacaceae in the Potoco flora; Tables 7.1, 7.3) without extensive highlands in the immediate vicinity. A few Eocene fruits, seeds, and palynomorphs have been described from Peru and Ecuador (Table 7.1), but there are no recently studied, published floras of sufficient size to make paleoenvironmental inferences or comparisons with the record from Argentina. There is an extensive deposit of petrified wood at Sexi, Cajamarca Province, in the Northern Andes of Peru, and Burnham (1994) has studied patterns of tropical leaf litter at Madre de Dios in Amazonian Peru that will be valuable in future investigations of megafossil floras.

Colombia

There are few published studies on Cretaceous megafossil floras from Colombia. Among them are wood, leaf, and pollen assemblages preserved in the eastern coastal basins (Pons, 1988;

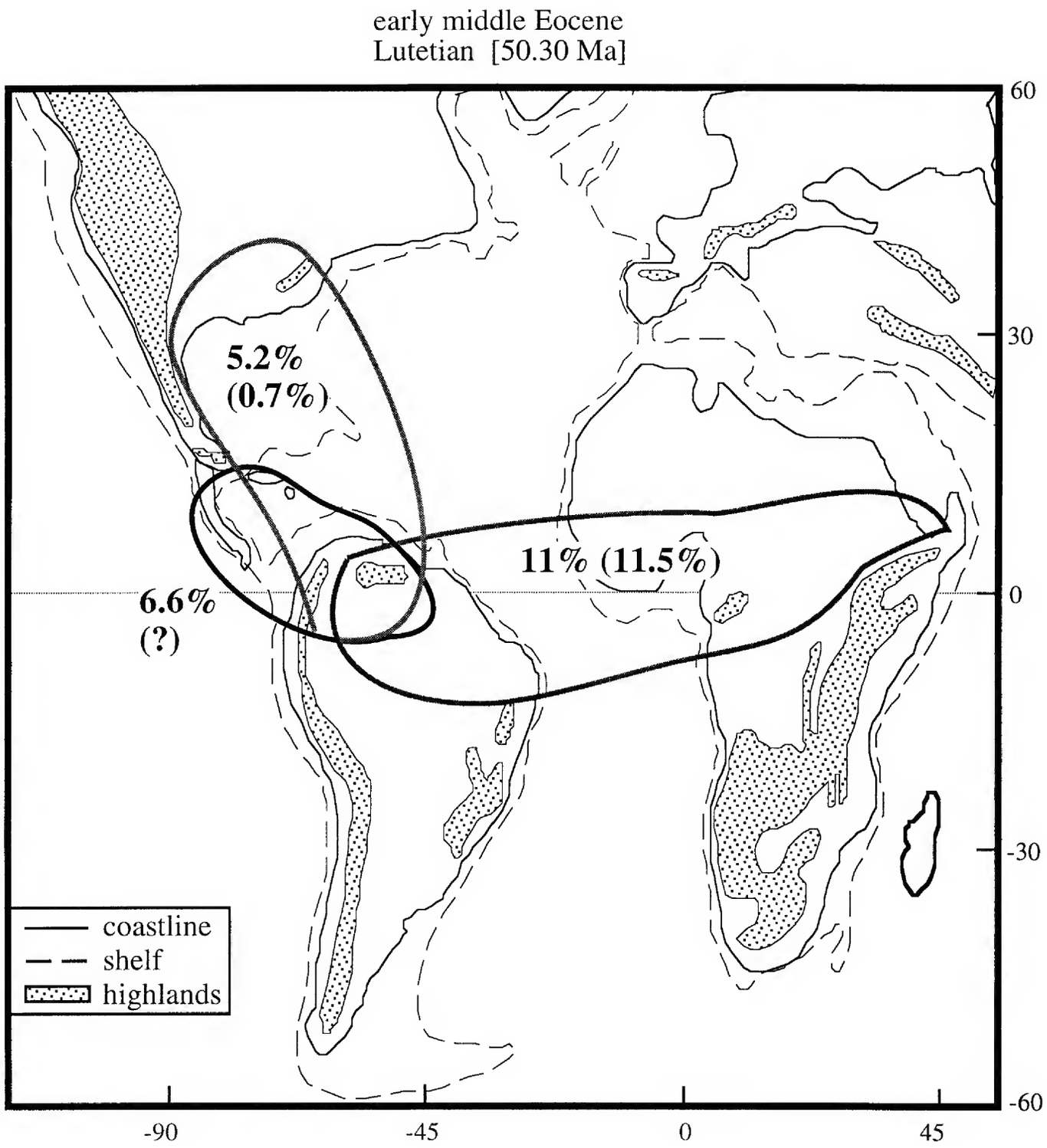


Figure 7.65. Percent shared similarity between northern South America and tropical Africa, Caribbean/Central America, and the Gulf Coast during the Paleocene (percentages in parentheses) and Eocene. From Jaramillo and Dilcher (2001); used with permission of Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, http://www.schweizerbart.de.

Tables 7.1, 7.3). They range in age from Barremian to Cenomanian and provide some insight into the Early Cretaceous vegetation and environments of northern South America. The principal trees were gymnosperms of the Araucariaceae and Podocarpaceae, and some cycadophytes, including many of the same genera found in the Early and Middle Cretaceous leaf and pollen floras of Argentina (e.g., *Brachyphyllum*). The understory was composed primarily of ferns and allied groups (Lycopodiaceae, Selaginellaceae, Cyatheaceae, Dicksoniaceae, Osmundaceae, Schizaeaceae), while the angiosperms were just becoming a prominent component. The floras suggest warm tropical climates, and they were deposited between evaporitic sequences indicating orogenically induced dry habitats. Local and periodically more widespread dry conditions are indicated by prolate, psilate, stephanocolpate (polyplicate) grains, some of which probably represent *Ephedra*. Overall, the Early and Middle Cretaceous of northern South America was a time of high sea levels, low to moderate elevations, frequent inundations, discontinuous land surfaces, and high temperatures. It was near the final stages of separation from northwestern Africa, after indirect near-connection with North America via Africa, and well after any direct connections with North America (Figs. 7.59–7.60).

Only a few megafossils of Paleogene age have been described from Colombia, mostly in the older literature, without formation names, and of uncertain age (many were assigned to the Eocene). There are seeds described as *Musa enseteformis* by Berry (1925a), subsequently transferred to *Ensete* (*E. enseteformis*), and an intriguing cast purported to be a banana fruit described by Huertas and van der Hammen (1953). Huertas (1970) reports retrieving *Musa*-like pollen from debris in the cavities of fossil seeds attributed to *Musa* and concludes that bananas were present in the Early and Late Cretaceous of Colombia. Musaceae in the order Zingiberales is not a particularly primitive (basal) group of monocots, and the origin of bananas is conventionally placed in southeastern Asia. Manchester and Kress (1993) have shown that Berry's specimens are recent remains, probably of the local *Ensete ventricosum*, and that the fruit is a concretion of nonbiological origin.

There are extensive assemblages of palynomorphs from late Paleocene to middle Eocene sediments in the Eastern Andes of Colombia (276 species; Jaramillo & Dilcher, 2001; Table 7.1). This includes the LPTM and EECL, but because most of the specimens cannot be assigned to modern taxa, it is not

possible to estimate the paleoclimates precisely except that the abundance of ferns and palms suggests warm and humid conditions. *Nothofagidites* was present but not abundant in the Eocene formations, and none of the northern temperate genera reported for the Cretaceous and Paleocene of southern South America in the older literature were identified from these even younger sediments farther to the north. *Pelliceria* (*Lanagiopollis crassa*), and possibly *Nypa* (*Spinozonocolpites* aff. *baculatus*) and *Hibiscus* (*Echiperiporites estelae*), document mangrove vegetation, including fringing mudflat association represented, for example, by the emergent aquatic *Crenea maritima* known back to the late Eocene (as *Verrutricolporites rotundiporis*; Germeraad et al., 1968). There were upland but no highland plants represented, and few desert elements, depending on how many polyplicate–stephanocolpate specimens (*Ephedripites*) reported throughout the literature are *Ephedra* versus Araceae (e.g., *Spathiphyllum*). Comparison of morphotypes of comparable ages from other regions of the world shows affinities with Africa (11.5% in the Paleocene, 11% in the Eocene), especially among the coastal elements, and less with North America, as expected (5.2%; Fig. 7.65). Now with more intense exploration for fossil floras in Colombia, new discoveries will undoubtedly increase the database significantly in the near future (e.g., Cerrejón).

Venezuela

A plant microfossil flora of ?Aptian to early Albian age is known from eastern Venezuela (Sinanoglu, 1983) that contains abundant ferns, six recognized forms of ephedroid pollen interpreted as growing on dry flats within a fluvial environment, and a single dicotyledon pollen type (*Retitricolpites vulgaris*) of unknown affinity. Sediments of the Cretaceous Río Acre and Marajó formations document marine incursions into the Amazon Basin, and there are tsunami deposits and iridium layers near Recife, Brazil, from the asteroid impact at Chicxulub that undoubtedly affected the K/T vegetation of northern South America. At the end of the Cretaceous, northern South America was separated from Africa and North America. Throughout the Tertiary, there were swamp, lagoon, and fluvial deposits in the proto-Amazon Basin, and until the middle Miocene, drainage was westward into the Pacific Ocean. Megafossil floras and several microfossil assemblages of Eocene age include mangrove elements (*Spinozonocolpite*s = *Nypa*, Arecaceae; *Psilatricolporites* = *Pelliceria*, Pelliceriaceae; *Retibrevitricolpites*, unknown affinity), and abundant palms and ferns (Tables 7.1, 7.3). The number of floras and identified elements with established biological affinities are so limited, however, that only a general impression is provided of a Late Cretaceous and Paleogene low-lying environment with uplands of moderate elevation, humid climates, locally edaphic dry areas, and tropical to warm-temperate vegetation.

Guianas

In the Guianas, the meager paleobotanical record is augmented by environmentally diagnostic bauxite deposits, like those discussed for Jamaica, as well as coals and lignites, all of which form under warm, humid, tropical environments (van der Hammen & Wijmstra, 1964). Consistent with this reconstruction is the fact that deposition of the bauxite is consistently preceded in the pollen diagrams by a rise in palm pollen (Wijmstra, 1971). On a finer time scale, there were environmental fluctuations because intermingled with the above deposits are evaporates such as gypsum and oxidized iron layers. These indicators of drier conditions, as well as intensified tectonic activity as the Caribbean Plate collided with the Bahamas Platform, become more prominent at the end of the middle Eocene.

Brazil

The same tectonic forces that produced the Mesozoic pull-apart sedimentary basins of Argentina generated others later along the northeastern coast of Brazil such as the Araripe Basin near Recife in the state of Ceará. Here the Crato Formation contains plant megafossils of Aptian or Albian age such as *Isoetites*, *Equisetites*, Schizaeaceae, Cycadales, Bennettitales, *Araucariostrobus* (Araucariaceae), *Brachyphyllum*, *Lindleycladus* (incertae sedis), Coniferales, and Gnetales (Kunzmann et al., 2004). Among the latter are remains attributed to the Welwitschiaceae (*Welwitschiophyllum brasiliense*, *Welwitschiella austroamericana*, *Welwitschiostrobus murili*; Dilcher et al., 2005), including *Cratonia cotyledon*, a seedling related to *Welwitschia* (Rydin et al., 2003). Microfossils from the Araripe Basin include an array of ephedroid pollen, originally assigned to *Equisetosporites* (De Lima, 1978, 1979, 1980, 1989), now placed in *Ephedripites* (Osborn et al., 1993). At about this time, the opening of the southern Atlantic Ocean had extended northward toward the equatorial zone, and the region of present-day Recife in eastern Brazil was near or appressed against the present-day Camaroon region of western Africa. This formed the climatically dry continental interior of west Gondwana. However, the presence of other plant fossils precludes assuming that continentality or coastal aridity provided extensive extremely dry conditions like those in the range of modern *Welwitschia* and *Ephedra*. The Crato Formation also has >30 taxa of angiosperms, constituting ~5% of the flora, belonging mostly to the magnoliid clade and basal eudicots (Mohr & Friis, 2000). They include *Trifurcatia flabellata* (possibly a monocot of seasonally dry habitats; Mohr & Rydin, 2002), *Arapipia florifera* (magnoliid; Mohr & Eklund, 2003), and *Endressinia brasiliana* (magnolialean; Mohr & Bernardes de Oliveira, 2004).

By the late Eocene, South America had been separated from Africa for ~50 Ma, and megafossil plants from the coastal Itaquaquecetuba Formation of the São Paulo Basin, including fossil logs up to 4 m in length, belong to a tropical evergreen forest fide Fittipaldi et al. (1989), rather than to semiarid vegetation as previously suggested when these deposits were, surprisingly, considered to be Quaternary in age (Bigarella, 1971; Ab'Saber, 1978; Suguio, 1980; Coimbra et al., 1983).

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. Suggested biological affinities and age assignments are according to the original authors unless otherwise indicated. Unpublished studies are cited in the References but are not included in the Table. Spores and reproductive structures (e.g., cleistothecia) of fungi, Pyrrophyta (dinoflagellates), diatoms, and other algae are often treated in separate publications, and only those cited in the references below are included here. Refs. = references, as follows, Argentina: 1 = Menéndez 1961, 2 = Frenguelli 1953a, 3 = Frenguelli 1943a, 4 = Frenguelli 1943b, 5 = Frenguelli 1953b, 6 = Anzótegui 1998 (Chenque now early Miocene, Table 7.1), 7 = Menéndez 1962, 8 = Barreda and Palamarczuk 2000c, 9 = Barreda and Caccavari 1992, 10 = Barreda et al. 1998, 11 = Caccavari and Barreda 2000, 12 = Mautino and Anzótegui 1998, 13 = Guler et al. 2001; Chile: 14 = Fuenzalida V. 1964, 15 = Nishida et al. 1988, 16 = Troncoso A. 1991, 17 = Troncoso A. and Romero 1993, 18 = Nishida 1970, 19a = Engelhardt 1891, 19b = Berry 1925b; Bolivia: 20 = Engelhardt 1887, 21 = Engelhardt 1894, 22 = Britton 1892, 23 = Berry 1917, 24 = Singewald and Berry 1922, 25 = Berry 1939b, 26 = Berry 1940, 27 = Graham et al. 2001; Peru: 28a = Berry 1919, 28b = Berry 1925c; Ecuador: 29 = Brown 1946, 30 = Berry 1945a (includes update of species in earlier study [Berry 1929d]), 31 = Engelhardt 1895; Colombia: 32 = Engelhardt 1895, 33 = Berry 1936b, 34 = Berry 1945b, 35 = Schönfeld 1947, 36 = Pons 1965, 1975, 1976, 1977, 1978, 1979, 1985 (all Mesa Formation), 37 = Pons 1969, 38 = Pons 1980, 39 = Wijninga 1996a; Venezuela: 40 = Berry 1922c, 41 = Berry 1937e, 42 = Berry 1939c, 43 = Lorente 1986; Trinidad: 44 = Berry 1925d, 45 = Kumar 1981; Brazil: 46 = Hollick and Berry 1924, 47 = Berry 1936c, 48 = Duarte 1956, 49 = Duarte 1958, 50 = Hoorn 1994a, b, c. Citations within the table are given in References, Chapter 7.

Argentina

Miocene

Megafossils

[1, Neuquén Province (Arroyo Puipucón, 6 km W of Aluminé), formation?, Miocene]

Ferns and allied groups: *Alsophilocaulis calveloi* (Cyatheaceae)

[2, La Lipela, Neuquén Province, formation?, Miocene]

Angiosperm (dicotyledon): *Eucalyptus patagonicus* (Myrtaceae)

[3, El Mirador, Chubut Province, formation?, Miocene]

Angiosperm (dicotyledon): *Casuarina patagonica* (Casuarinaceae)

[4, Morro Revancha, Río Negro Province, formation?, Miocene]

Angiosperms (dicotyledons): *Lomatia occidentalis* (Proteaceae), *L. patagonica* (Proteaceae)

[5, Río Chalia, Santa Cruz Province, formation?, Miocene]

Ferns and allied groups: *Equisetites* (Equisetaceae). Gymnosperm: *Fitzroya tertiaria* (Cupressaceae). Angiosperms (dicotyledons): *Bignonites chalianus* (Bignoniaceae), *Laurophyllum kurtzi* (Lauraceae), *Myrcia acutifolia*, *M. santacruzensis* (Myrtaceae), *Schinopsis? dubia* (Anacardiaceae). Incertae sedis: *Phyllites*

[6, Río Calchaquí, Salta Province, Palo Pintado Formation, late Miocene]

Angiosperms (dicotyledons): *Ficus tressensii* (Moraceae), *Nectandra saltensis* (Lauraceae), *Schinus herbstii* (Anacardiaceae)

Pliocene

Megafossils

[7, Tiopunco, Valley of Santa María, Tucumán Province, formation?, Pliocene]

Angiosperm (dicotyledon): *Acacioxylon o'donellii* (Leguminosae)

Microfossils

[8, Monte Observación–Monte Entrada sections, Santa Cruz Province, Monte León Formation, probably early Miocene]

Algae: *Botryococcus*, *Pediastrum*. Ferns and allied groups: *Azolla*, *Cyatheacidites annulatus* (Lophosoriaceae), *Ischyosporites areapunctatis* (Cyatheaceae), *Muricingulisporis chenquensis* (Pteridaceae). Gymnosperms: Araucariaceae, *Equisetosporites claricristatus* (Ephedraceae), Podocarpaceae. Angiosperms (monocotyledons): *Arecipites subverrucatus* (Palmae), *Cyperaceaepollis neogenicus* (Cyperaceae), *Graminidites* (Gramineae), *Sparganiaceaepollenites barungensis* (Sparganiaceae), *Sparganium*. Angiosperms (dicotyledons): *Baumannipollis variaperturatus* (Malvaceae), *Chenopodipollis chenopodiaceoides* (Amaranthaceae–Chenopodiaceae [chenoam]), *Corsinipollenites atlantica* (Onagraceae), Fagaceae, *Glencopollis ornatus*, *Lactoris* (Lactoridaceae), *Malvacipolloides comodoroensis* (Malvaceae), *Milfordia argentina*, *Multisiapollis viteauensis* (Compositae), *Quintiniapollis striatulosa*, *Rhoipites cienaguensis*, *Senipites patagonica* (Symplocaceae), *Tricolpites trilobatus*, *Tubulifloridites antipodica* (Compositae)

[9, Golfo de San Jorge Basin, Chubut Province, Chenque Formation, early Miocene; Table 7.1]

Angiosperms (dicotyledons): *Acaciapollenites myriosporites* (Leguminosae), *Polyadopollenites* (Leguminosae)

[10, Valle del Cura, San Juan Province, Yeso Series, Miocene, probably middle Miocene]

Algae: *Botryococcus*, *Pediastrum*. Bryophyta: *Ricciaesporites* (*Riccia*). Ferns and allied groups: *Biretisporites*, *Deltoidospora*, *Leiotriletes*. Gymnosperms: *Equisetosporites claricristatus*, *E. lusaticus* (Ephedraceae), *E. notensis*, *Podocarpidites elegans*, *P.* cf. *ellipticus* (Podocarpaceae). Angiosperms (monocotyledons): *Cyperaceaepollis neogenicus* (Cyperaceae), *Graminidites* (Gramineae). Angiosperms (dicotyledons): *Baumannipollis variaperturatus* (Malvaceae), *Chenopodipollis chenopodiaceoides* (Amaranthaceae–Chenopodiaceae), *Lymingtonia*? (Nyctaginaceae–Portulaceae), *Malvacipollis subtilis* (Euphorbiaceae), *Malvacipolloides comodoroensis* (Malvaceae), *Margocolporites vanwijhei* (Leguminosae, Caesalpinioideae), *Mutisiapollis viteauensis* (*Mutisia*, Compositae), *Myrtaceidites* (Myrtaceae), *Nothofagidites acromegacanthus*, *N. saraensis* (Fagaceae), *Orapollis* (Amaranthaceae), *Poluspissusites* (Goodeniaceae), *Polyadopollenites*? (Leguminosae, Mimosoideae, *Calliandra*), *Polyorificites*, *Proteacidites* (Proteaceae), *Rhoipites baculatus*, *R. cienaguensis*, *Senipites patagonica* (Symplocaceae), *Striatricolporites gamerroi* (Anacardiaceae), *Tetracolporites spectabilis* (Meliaceae), *Tubliforidites antipodica* (Compositae)

[11, Cordillera de La Brea, Valle del Cura, San Juan Province, La Ollita Formation, middle Miocene]

Angiosperm (dicotyledon): *Calliandra* (Leguminosae, Mimosoideae)

[12, Vallecito, Catamarca Province, Chiquimil Formation, late Miocene]

Ferns and allied groups: *Dictyophyllidites chiquimilense*, *Muricingulisporis verrucosus* (Pteridaceae)

[13, Cuenca del Colorado Well Cx-1, Buenos Aires Province, Barranca Final Formation, late Miocene]

Bryophyta: *Ricciaesporites transdanubicus* (Ricciaceae). Ferns and allied groups: *Azolla* (Salviniaceae), *Foveotriletes* cf. *labrus* (Cyatheaceae?), *Laevigatosporites ovatus*, *Triletes* cf. *tuberculiformis*. Gymnosperms: *Equisetosporites claricristatus*,

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. *(Continued)*

E. fusiformis, *E. lusaticus*, *E. notensis* (Ephedraceae), *Podocarpidites marwickii*, *P. rugulosus* (Podocarpaceae). Angiosperms (monocotyledons): *Cyperaceaepollis neogenicus* (Cyperaceae), *Graminidites* (Gramineae), *Sparganiaceaepollenites barungensis* (Sparganiaceae). Angiosperms (dicotyledons): *Acaciapollenites myriosporites* (Leguminosae, Mimosoideae), *Ailanthipites* cf. *marginatus*, *A.* cf. *nonprolatus* (Anacardiaceae), *Baumannipollis chubutensis* (Malvaceae), *Chenopodipollis chenopodiaceoides* (Amaranthaceae–Chenopodiaceae), *Corsinipollenites* cf. *exinitenuis* (Onagraceae), *Cricotriporites guianensis*, *Haloragacidites amolosus* (Haloragidaceae, *Haloragis*), *H. harrisii* (Casuarinaceae, Myricaceae), *H. myriophylloides* (Haloragidaceae, *Myriophyllum*), *Malvacipolloides comodoroensis* (Malvaceae), *Myrtaceidites mesonesus*, *M. verrucosus* (Myrtaceae), *Nothofagidites dorotensis*, *N. saraensis* (Fagaceae), *Rhoipites* cf. *cienaguensis*, *Striatricolporites gamerroi* (Anacardiaceae), *Tricolpites reticulatus* (Gunneraceae), *T. trioblatus* (Scrophulariaceae), *T.* sp. 1 (Cruciferae), *Trivestivulopollenites* (Betulaceae), *Tubulifloridites antipodica*, *T. simplis* (Compositae), *T. viteauensis* (Compositae, *Mutisia*), *T.* sp. (Compositae, *Ambrosia*)

Chile

Miocene

Megafossils

[14, El Arrayán, Santiago, formation?, Oligo–Miocene]

Angiosperms (dicotyledons): *Alnus* (Betulaceae), *Cassia argentinensis* (Leguminosae), *Cissus pichinleufuensis* (Vitaceae), *Fagus* [*Nothofagus*] *subferruginea* (Fagaceae), *Myrcia reticulato-venosa* (Myrtaceae), *Nothofagus crenulata*, *N. lanceolata* (Fagaceae), *Persea* (Lauraceae), *Zanthoxylo*[*u*]*n* (Rutaceae)

[15, Cerro Dorotea, Ultima Esperanza, Fuego Island, Filaret Formation, Miocene]

Angiosperms (dicotyledons): *Aextoxicoxylon harambouri* (Aexotoxicaceae), *Laurelites doroteaensis* (Monimiaceae), *Laurinoxylon uniseriatum*, *Myrceugenellites maytenoides* (Myrtaceae)

[16, Matanzas, Navidad Formation, Miocene]

Ferns and allied groups: *Asplenium* (Aspleniaceae), *Blechnum* (Blechnaceae), cf. *Ctenitis* (Dryopteridaceae), *Equisetum* (Equisetaceae), cf. *Lophosoria* (Lophosoriaceae). Incertae sedis: *Filicites* sp. 1–4. Gymnosperms: *Araucaria* (Araucariaceae), *Podocarpus* (Podocarpaceae), *Saxegothopsis* (Podocarpaceae). Angiosperm (monocotyledon): *Dioscorea* (Dioscoreaceae). Angiosperms (dicotyledons): *Agonis* (Myrtaceae), *Amomyrtus* (Myrtaceae), *Aulomyrcia* (Myrtaceae), *Berberis* (Berberidaceae), *Boquila* (Lardizabalaceae), *Caldcluvia* (Cunoniaceae), *Callistemon* (Myrtaceae), *Desfontainia* (Loganiaceae), *Doryphora* (Monimiaceae), *Laurophyllum* (Lauraceae), Malpighiaceae?, *Melastomophyllum* (Melastomataceae), *Mitraria* (Gesneriaceae), *Myrceugenia* (Myrtaceae), *Myrcia* (Myrtaceae), *Nothofagus gonzalezii* (Fagaceae), *Ocotea* (Lauraceae), *Ovidia* (Thymelaeaceae), *Persea* (Lauraceae), *Phoebe* (Lauraceae), *Senna* (Leguminosae), *Weinmannia* (Cunoniaceae). Incertae sedis: *Phyllites* sp. 1–5

[17, Matanzas, central-western Chile, Navidad Formation, Miocene]

Gymnosperms: *Araucaria* (Araucariaceae), *Austrocedrus* (Cupressaceae), *Dacrydium* (Podocarpaceae), *Podocarpus* (Podocarpaceae), *Saxegothopsis* (Podocarpaceae)

[18, various localities, Navidad, 100 km SW Santiago, formations?, various ages, one Miocene]

Gymnosperm: *Araucarioxylon chilense* (Araucariaceae)

[19a, Coronel-Lota, 37°S near Concepción, formation?, Late Tertiary; note unlikely identifications of *Sequoia* and *Fagus* (= *Nothofagus*?), see Table 7.1, Ref. 58]

Algae: *Chondrites subsimplex*. Ferns and allied groups: *Adiantides borgoniana*, *Blechnum antediluvianum* (Blechnaceae), *Pecopteris buhsei* (undeterminable fragment of Paleozoic fern-like foliage), *Pteris cousiniona* (Pteridaceae). Gymnosperms: *Ephedra* (Ephedraceae), *Sequoia chilensis* (Taxodiaceae [?]), *Zamia tertiaria* (Cycadaceae). Angiosperms (monocotyledons): *Flabellaria schwageri* (Palmae; name now used for a genus of the Malpighiaceae, probably *Flagellaria*), *Sabal ochseniusi* (Palmae). Angiosperms (dicotyledons): *Acrodiclidium oligocaenicum* (Lauraceae), *Allamanda crassostipitata* (Apocynaceae), *Ampelodaphne grandifolia* (Lauraceae), *An*(*n*)*ona coronelensis*, *A. speciosa* (Annonaceae), *Antidaphne lotensis* (Santalaceae), *Apocynophyllum chilense* (Apocynaceae), *Ardisia crassifolia* (Myrsinaceae), *Arthante* [*Artanthe*, = *Piper*] *geniculatoides* (Piperaceae), *Banara cuadrae* (Bixaceae, Flacourtiaceae), *Benettia grosse-serrata* (Compositae), *Bignonia gigantifolia* (Bignoniaceae), *Bombaciphyllum opacum* (Bombacaceae), *Bombax firmifolium*, *B. playense* ([Bombacaceae], Malvaceae original author), *Camphoromoea speciosa* (Lauraceae), *Casearia oliganthoides*, *C. piparoides*, *C. spinuloso-serrata* (Flacourtiaceae), *Combretum oblongifolium* (Combretaceae), *Copaifera reticulata* (Leguminosae), *Cordia pulchra* (Boraginaceae–Cordiaceae), *Coussapoa quinquenervis* (Urticaceae), *Coussarea membranacea* (Rubiaceae), *Desmodium obliquum* (Leguminosae), *Doliocarpus oblongifolia*, *D.* (?) *serrulata* (Dilleniaceae), *Empedoclea repando-serrata* (Dilleniaceae), *Erythrochyton grandifolium* (Rutaceae), *Fagus magelhaenica* (Fagaceae [*Nothofagus*?]), *Goeppertia ovalifolia*, *G. spectabilis* (Lauraceae), *Gomphia firmifolia* (Ochnaceae; Africa, India, SE Asia), *Gouatteria tenuinervis* (Rubiaceae), *Haemadictyon tenuifolium* (Apocynaceae), *Hoffmannia protogaea* (Rubiaceae), *Ilex subtilinervis* (Aquifoliaceae), *Laetia transversonervis* (Bixaceae), *Laurophyllum actinodaphnoides* (Lauraceae), *Lecythis neriifolia* (Myrtaceae), *Leguminosites copaiferaeoides* (Leguminosae), *L. erythrinoides* (Leguminosae), *Mallotus* (?) *platanoides* (Euphorbiaceae), *Maytenus araucensis*, *M. magnoliaefolia* (Celastraceae), *Mespilodaphne longifolia* (Lauraceae), *Moschoxylun falcatum*, *M. tenuinerve* (Meliaceae), *Myrcia* (*Aulomyrcia*) *costatoides*, *M. deltoidea*, *M.* (*Cryptomyrcia*) *nitens*, *M. reticulato-venosa* (Myrtaceae), *Myrciaria acuminata* (Myrtaceae), *Myrciophyllum amgiguacoides* (Myrtaceae), *Myristica fossilis* (Myristicaceae), *Nectandrophyllum* (Lauraceae), *Omphalea ficiformis* (Euphorbiaceae), *Patrisia eocenica* (Asclepiadaceae), *Persea macrophylloides*, *P. microphylla* (Lauraceae), *Phoebe elliptica*, *P. lanceolata* (Lauraceae), *Pilocarpus saavedrai* (Rutaceae), *Psidium membranaceum* (Myrtaceae), *Psittacanthus crassifolius* (Loranthaceae), *Psychotria grandifolia* (Rubiaceae), *Sabicea* (?) *elliptica* (Rubiaceae), *Sapindus acuminatus* (Sapindaceae), *Styrax coriacea*, *S. glabratoides* (Styracaceae), *Tecoma serrata* (Bignoniaceae), *Tetracera elliptica*, *T. rhamnoides* (Dilleniaceae), *Tetraplandra longifolia* (Euphorbiaceae), *Thevetia angustifolia* (Apocynaceae), *Thouinia philippii* (Sapindaceae), *Ticorea foetidoides* (Rutaceae), *Triumfetta irregulariter-serrata* (Tiliaceae), *Vochysia dura* (Vochysiaceae), *Zanthoxylon inaequabile*, *Z. tenuifolium* (Rutaceae). Incertae sedis: *Carpolites cycaeformis*, *C. guilielmaeoides*, *Phyllites acuto-serratus*, *P. alsodeiaecoides*, *P. aspidospermaeoides*, *P. banisteriaeoides*, *P. coccolobaefolia*, *P. cycaeformis*, *P. repandus*, *P. sauraujaeoides*, *P. ternstroemiaeoides*, *P. triplarioides*

[19b, Mirador Mesa (Mirhoja), N of Río Chubut, Chubut Province, formation?, Miocene]

Angiosperm (monocotyledon): *Poacites* (Gramineae). Angiosperms (dicotyledons): *Arrabidaea patagonica* (Bignoniaceae), *Banara prehernandiensis* (Flacourtiaceae), *Bignonites ovatus* (Bignoniaceae), *Celtis ameghenoi* (Ulmaceae), *Cupania grosse-serrata*, *C. inserta*, *C. latifolioides* (Sapindaceae), *Erythroxylon cuneifolioides* (Erythroxylaceae), *Faramea miocenica* (Rubiaceae), *Icica tertiaria* (Burseraceae), *Leguminosites patagonicus* (Leguminosae), *Lomatites occidentalis* (Proteaceae), *Malvacarpus tertiarius* (Malvaceae), *Maytenus latifolioides* (Celastraceae), *Myrcia chubutensis* (Myrtaceae), *Myrica mira* (Myricaceae), *Nectandra patagonica* (Lauraceae), *Peumus clarki* (Monimiaceae), *Rhamnidium* (?) *patagonicum*, *R. preglabrum* (Rhamnaceae), *Sapindus argentinus* (Sapindaceae), *Schinopsis patagonica* (Anacardiaceae), *Schmidelia eduliforma*, *S. graciliforma*, *S. proedulis* (Sapindaceae), *Sterculia patagonica* (Sterculiaceae), *Strychnos mirhojana* (Loganiaceae), *Styrax acuminatiformis* (Styracaceae), *Tetracera patagonica* (Dilleniaceae). Incertae sedis: *Carpolithus bivascularis*, *C. mirhojanus*, *C. patagonicus*, *Phyllites sloaneaformis*

Bolivia

Megafossils

[20, Cerro de Potosí, formation?, Late Tertiary, included under Miocene in Appendix 2]

Angiosperms (dicotyledons): *Cassia chrysocarp*[*i*]*oides*, *C. cristoides*, *C. ligustrinoides* (Leguminosae), *Myrcia banksioides* (Myrtaceae), *Sweetia tertiaria* (Leguminosae, = *Galactia*). Incertae sedis: *Phyllites franckei*

[21, Cerro de Potosí, formation?, Late Tertiary, included under Miocene in Appendix 2]

Ferns and allied groups: *Acrostichum linearifolium* (Pteridaceae), *Gymnogramme*

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. *(Continued)*

(?) sp. (= *Hemionitis*; now distributed among several genera, Pteridaceae), *Lomariopsis tertiaria* (Dryopteridaceae), *Pecopteris* (undeterminable fragment of Paleozoic fern-like foliage). Gymnosperms: *Podocarpus fossilis* (Podocarpaceae). Angiosperm (monocotyledon): *Poacites* (Gramineae). Angiosperms (dicotyledons): *Acacia dimidiato-cordata*, *A. tenuifolia*, *A. uninervifolia* (Leguminosae), *Caesalpinia gmehlingi* (Leguminosae), *Calliandra obliqua*, *C. ovatifolia* (Leguminosae), *Capparis multinervis* (Capparidaceae), *Cassia chrysocarp[i]oides*, *C. ligustrinoides*, *C. membranacea*, *C. obscura*, *C. rigidulifolia* (Leguminosae), *Dalbergia antiqua*, *D. chartacea* (Leguminosae), *Desmodium ellipticum* (Leguminosae), *Drepanocarpus franckei* (Leguminosae), *Enterolobium grandifolium*, *E. parvifolium* (Leguminosae), *Gaylussacia tertiaria* (Ericaceae), *Hedysarum bolivianum* (Leguminosae), *Inga ochseniusi* (Leguminosae), *Lonchocarpus obtusifolius* (Leguminosae), *Machaerium eriocarpoides* (Leguminosae), *Mimosa arcuatifolia*, *M. montanoides* (Leguminosae), *Mimosites* (Leguminosae), *Myrica banksioides*, *M. wendtii* (Myricaceae), *Myricophyllum* (Myricaceae), *Peltophorum membranaceum* (Leguminosae), *Pithecolobium tertiarium* (Leguminosae), *Platypodium potosianum* (Leguminosae), *Ruprechtia braunii* (Polygonaceae), *Sweetia tertiaria* (Leguminosae), *Weinmannia brittoni* (Cunoniaceae). Incertae sedis: *Antholithes quinquepartitus*, *Carpolites ovoideus*, *Leguminosites* (?) *globularis*, *Mimosites linearis*, *Phyllites franckei*

[22, Potosí, Bolivia, formation?, Late Tertiary, included under Miocene in Appendix 2]

Angiosperms (dicotyledons): *Amicia antiqua* (Leguminosae), *Cassia chrysocarp[i]oides*, *C. cristoides*, *C. ligustrinoides*, *C. wendtii* (Leguminosae), *Cuphea antiqua* (Lythraceae), *Escallonia wendtii* (Saxifragaceae), *Euphorbia* (?) (Euphorbiaceae), *Myrica banksioides*, *M. engelhardtii*, *M. potosina*, *M. wendtii* (Myricaceae), *Passiflora* (?) *canfieldi* (Passifloraceae), *Porlieria tertiaria* (Zygophyllaceae), *Swertia tertiaria* (Leguminosae; *Sweetia* [?], not *Swertia* of the Gentianaceae), *Terminalia antiqua* (Combretaceae). Incertae sedis: *Phyllites franckii*

[23, Corocoro, Potosí, formations?, Pliocene; see also Berry, 1922d]

Ferns and allied groups: *Acrostichum linearifolium* (Pteridaceae), *Gymnogramma* (= *Hemionitis*; now distributed among several genera, Pteridaceae), *Lomariopsis tertiaria* (Dryopteridaceae), *Pecopteris* (undeterminable fragment of Paleozoic fern-like foliage), *Polystichum bolivianum* (Dryopteridaceae). Gymnosperm: *Podocarpus fossilis* (Podocarpaceae). Angiosperms (monocotyledons): Gramineae—*Festuca*, *Phragmites*, *Poacites*, Palmae—*Palmophyllum*. Angiosperms (dicotyledons): *Acacia dimidiato-cordata*, *A. tenuifolia*, *A. uninervifolia* (Leguminosae), *Aeschynomene bolivianum* (Leguminosae), *Amicia antiqua* (Leguminosae), *Apocynophyllum potosianum* (Apocynaceae), *Bauhinia potosiana* (Leguminosae), *Caesalpinia gmehlingi*, *C. potosianus*, *C. sessilifolioides* (Leguminosae), *Calliandra obliqua*, *C. ovatifolia* (Leguminosae), *Capparis multinervis* (Capparidaceae), *Cassia chrysocarpoides*, *C. cristoides*, *C. cultrifoliaformis*, *C. franckei*, *C. ligustrinaformis*, *C. membranacea*, *C. obscura*, *C. rigidulifolia*, *C. singewaldi*, *C. wendtii* (Leguminosae), *Copaifera corocoriana*, *C. potosiana* (Leguminosae), *Cuphea antiqua* (Lythraceae), *Cypselites potosianus* (Compositae), *Dalbergia* (?) *antiqua*, *D. chartacea*, *D. potosiana* (Leguminosae), *Desmodium ellipticum* (Leguminosae), *Drepanocarpus franckei* (Leguminosae), *Enterolobium grandifolium*, *E. parvifolium* (Leguminosae), *Escallonia wendtii* (Saxifragaceae), *Euphorbia* (?) (Euphorbiaceae), *Gaylussacia tertiaria* (Ericaceae), *Inga ochseniusi* (Leguminosae), *Jacaranda potosiana* (Bignoniaceae), *Leguminosites* (?) *globularis* (Leguminosae), *Lonchocarpus obtusifolius* (Leguminosae), *Machaerium eriocarpoides*, *M. milleri* (Leguminosae), *Mimosa arcuatifolia*, *M. montanoides* (Leguminosae), *Mimosites engelhardti* (Leguminosae), *Myrica banksioides*, *M. engelhardtii*, *M. wendtii* (Myricaceae), *Myricophyllum* (Myricaceae), *Myrteola potosiana* (Myrtaceae), *Passiflora canfieldi* (Passifloraceae), *Peltophorum membranaceum* (Leguminosae), *Pithecolobium brittonianum*, *P. tertiarium* (Leguminosae), *Platypodium potosianum* (Leguminosae), *Porlieria tertiaria* (Zygophyllaceae), *Rubiacites nummularioides* (Rubiaceae), *Ruprechtia braunii* (Polygonaceae), *Sweetia tertiaria* (Leguminosae), *Terminalia antiqua*, *T. singewaldi* (Combretaceae), *Weinmannia brittonii*, *W. potosina* (Cunoniaceae). Incertae sedis: *Antholithus quinquepartita*, *Carpolithus engelhardti*, *C.* sp. 1–5, *C. viornaformis* (Ranunculaceae?)

[24, Corocoro copper district, Pacajes Province, Department of La Paz, Vetas (Pliocene), Ramos (Plio–Pleistocene) formations]

Ferns and allied groups: *Polystichum bolivianum* (Dryopteridaceae). Gymnosperm: *Podocarpus fossilis* (Podocarpaceae). Angiosperms (dicotyledons): *Acacia uninervifolia* (Leguminosae), *Amicia antiqua* (Leguminosae), *Calliandra obliqua* (Leguminosae), *Cassia ligustrinaformis* (Leguminosae), *C. singewaldi* (Leguminosae), *Copaifera corocoriana* (Leguminosae), *Dalbergia antiqua* (Leguminosae), *Dodonaea viscosaformis* (Sapindaceae), *Drepanocarpus franckei* (Leguminosae), *Enterolobium grandifolium* (Leguminosae), *Machaerium eriocarpoides* (Leguminosae), *Mimosa arcuatifolia* (Leguminosae), *Mimosites engelhardti* (Leguminosae), *Osteomeles pliocenica* (Rosaceae), *Peltophorum membranaceum* (Leguminosae), *Rubiacites nummularioides* (Rubiaceae), *Ruprechtia braunii* (Polygonaceae), *Terminalia singewaldi* (Combretaceae), *Vaccinium pontzuelum* (Ericaceae). Incertae sedis: *Carpolithus baulti*

[25, Potosí, Corocoro series, Pliocene]

Ferns and allied groups: *Acrostichum linearifolium* (Pteridaceae), *Goniopteris* (Thelypteridaceae; *Pecopteris* of Engelhardt Ref. 21 above), *Gymnogramme(a)* (= *Hemionitis*; now distributed among several genera, Pteridaceae), *Lomariopsis tertiaria* (Dryopteridaceae), *Polystichum bolivianum* (Dryopteridaceae). Gymnosperms: *Podocarpus boliviensis*, *P. fossilis* (Podocarpaceae). Angiosperms (monocotyledons): Gramineae—*Festuca*, *Phragmites*, *Poacites*, Palmae—*Palmophyllum*. Angiosperms (dicotyledons): *Acacia dimidiato-cordata*, *A. tenuifolia*, *A. uninervifolia* (Leguminosae), *Aeschynomene bolivianum* (Leguminosae), *Amicia antiqua* (Leguminosae), *Apocynophyllum potosianum* (Apocynaceae), *Bauhinia potosiana* (Leguminosae), *Caesalpinia gmehlingi*, *C. potosianus*, *C. sessilifoliodes* (Leguminosae), *Calliandra obliqua*, *C. ovatifolia* (Leguminosae), *Capparis multinervis* (Capparidaceae), *Cassia chrysocarpoides*, *C. cristoides*, *C. cultrifoliaformis*, *C. franckei*, *C. ligustrinaformis*, *C. membranacea*, *C. obscura*, *C. rigidulifolia*, *C. singewaldi*, *C. wendtii* (Leguminosae), *Copaifera corocoriana*, *C. potosiana* (Leguminosae), *Cuphea antiqua* (Lythraceae), *Cypselites potosianus* (Compositae), *Dalbergia antiqua* (?), *D. chartacea*, *D. potosiana* (Leguminosae), *Desmodium ellipticum* (Leguminosae), *Dodonaea viscosaformis* (Sapindaceae), *Drepanocarpus franckei* (Leguminosae), *Duvaua pliocenica* (Anacardiaceae), *Enterolobium grandifolium*, *E. parvifolium* (Leguminosae), *Escallonia wendtii* (Saxifragaceae), *Euphorbia* (?) (Euphorbiaceae), *Gaylussacia ovata*, *G. tertiaria* (Ericaceae), *Hoffmannia boliviana* (Rubiaceae), *Inga ochseniusi* (Leguminosae), *Jacaranda potosiana* (Bignoniaceae), *Leguminosites* (?) *globularis* (Leguminosae), *Lonchocarpus obtusifolius* (Leguminosae), *Machaerium eriocarpoides*, *M. milleri* (Leguminosae), *Mimosa arcuatifolia*, *M. montanoides* (Leguminosae), *Mimosites engelhardti*, *M. linearis* (Leguminosae), *Myrica banksioides* (Myricaceae), *Myricophyllum* (Myricaceae), *Myrteola potosiana* (Myrtaceae), *Osteomeles pliocenica* (Rosaceae), *Passiflora canfieldi* (Passifloraceae), *Peltophorum membranaceum* (Leguminosae), *Piperites potosiensis* (Piperaceae), *Pithecolobium brittonianum*, *P. tertiarium* (Leguminosae), *Platypodium potosianum* (Leguminosae), *Porlieria tertiaria* (Zygophyllaceae), *Rubiacites nummularioides* (Rubiaceae), *Ruprechtia braunii* (Polygonaceae), *Sweetia tertiaria* (Leguminosae), *Terminalia antiqua*, *T. singewaldi* (Combretaceae), *Vaccinium pontzuelum* (Ericaceae), *Weinmannia brittoni*, *W. potosina* (Cunoniaceae). Incertae sedis: *Antholithus quinquepartita*, *Carpolithus engelhardti*, *C. viornaformis* (Ranunculaceae?), *C.* sp. 1–5, *Phyllites nymphaeacites*

[26, Agua Salada, 25 km NE of Yacuíba, formation?, Pliocene]

Angiosperm (dicotyledon): *Cusparia yacuibana* (Rutaceae)

Microfossils

[27, Pislepampa, Altiplano, formation?, Mio–Pliocene]

Ferns and allied groups: *Cnemidaria* (Cyatheaceae), *Cyathea* types 1–3 (Cyatheaceae), *Danaea* (Marrattiaceae), *Grammitis* (Grammitidaceae), *Hymenophyllum* (Hymenophyllaceae), *Isoetes* (Isoetaceae), *Lycopodium* types 1–3 (Lycopodiaceae), *Pteris* (Pteridaceae). Gymnosperm: *Podocarpus–Prumnopitys*. Angiosperms (monocotyledons): Gramineae, Palmae. Angiosperms (dicotyledons): *Cavanillesia* (Bombacaceae), Compositae types 1–3, Ericaceae, *Ilex* (Aquifoliaceae), cf. *Oreopanax* (Araliaceae), cf. *Pereskia* (Cactaceae), *Tetrorchidium* (Euphorbiaceae)

Peru

Miocene

Megafossils

[28a, Tumbes, formation?, Miocene (Burdigalian)]

Angiosperms (monocotyledons): *Bambusium stubeli* (Gramineae), *Iriartites*

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. *(Continued)*

tumbezensis (Palmae), *Stenospermation columbiense* (Araceae). Angiosperms (dicotyledons): *An(n)ona winslowiana* (Annonaceae), *Banisteria incerta* (Malpighiaceae), *Condaminea grandifolia* (Rubiaceae), *Ficus winslowiana* (Moraceae), *Guatteria culebrensis* (Annonaceae), *Mespilodaphne tumbezensis* (Lauraceae), *Persea macrophylloides* (Lauraceae), *Styrax lanceolata* (Styracaceae), *Tapirira lanceolata* (Anacardiaceae), *Trigonia varians* (Trigoniaceae), *Vochysia retusifolia* (Vochysiaceae)

[28b, Río Aguaytía tributary of the Río Ucayali, Loreto Region, formation?, late Miocene or Pliocene]

Angiosperms (dicotyledons): *Banisteria bassleri* (Malpighiaceae), *Bignonia neogenia* (Bignoniaceae), *Bignonites americanum* (Bignoniaceae), *Cassia aguaytiensis*, *C. bassleri* (Leguminosae), *Guazuma tertiaria* (Sterculiaceae), *Momisia asperulaformis*, *M. iguanaeaformis* (Ulmaceae), *Pithecolobium presaman* (Leguminosae), *Tetracera tertiaria* (Dilleniaceae), *Trema micranthaformis* (Ulmaceae), *Vallea prepubescens* (Elaeocarpaceae)

Ecuador

Miocene

Megafossils

[29, Punta Gorda, Esmeraldas Province, Punta Gorda Formation, Mio–Pliocene]

Angiosperm (dicotyledon): *Juglans linki* (Juglandaceae)

[30, Loja Basin, formation?, Mio–Pliocene]

Bryophyta, Musci: *Muscites*. Ferns and allied groups: *Elaphoglossum carrioni* (Dryopteridaceae), *Filicites lojanus* (Polypodiaceae), *Goniopteris cochabambensis*, *G. lojana* (Polypodiaceae), *Lygodium bifidum* (Schizaeaceae). Gymnosperm: *Zamia* (Cycadaceae). Angiosperms (monocotyledons): Palmae, *Poacites magnus* (Gramineae), *Scleria wolfi* (Cyperaceae). Angiosperms (dicotyledons): *Alchornea swartzi* (Euphorbiaceae), *Artanthe geniculatoides* (Piperaceae), *Banisteria aceroides* (Malpighiaceae), *Bauhinia ecuadorensis* (Leguminosae), *Bignonia tertiaria* (Bignoniaceae), *Bombax retusifolium* (Bombacaceae), *Bumelia lojana* (Sapotaceae), *Caesalpinia subdimidiata* (Leguminosae), *Camphoromaea speciosa* (Lauraceae), *Capparis verrucosafolia* (Capparidaceae), *Cassia bassleri*, *C. dimidiatolinearis*, *C. linearifolia*, *C. longifolia* (Leguminosae), *Couratari tertiaria* (Lecythidaceae), *Couroupita tertiaria* (Lecythidaceae), *Coussapoa carrioni* (Moraceae), *Enckea columbrinoides* (Piperaceae), *Eugenia ovalifolia* (Myrtaceae), *Exostema precaribaeum* (Rubiaceae), *Hiraea cyclosperma* (Malpighiaceae), *Hirtella lojana* (Rosaceae), *Inga engelhardti*, *I. lojana* (Leguminosae), *Leguminosites cassioides*, *L. engelhardti*, *L. grandis* (Leguminosae), *Lonchocarpus engelhardti* (Leguminosae), *Luhea tertiaria* (Tiliaceae), *Macrolobium tenuifolium* (Leguminosae), *Melastomites* (Melastomataceae), *Melochia carrioni* (Sterculiaceae), *Mespilodaphne lojana* (Lauraceae), *Mimusops miocenica* (Sapotaceae), *Momisia ecuadorensis*, *M. iguanaeaformis* (Ulmaceae), *Myrcia antediluviana*, *M. cajamarcana* (Myrtaceae), *Myrciaria tenuifolia* (Myrtaceae), *Myristica fossilis* (Myristicaceae), *Myrsine eomyricoides* (Myrsinaceae), *Nectandra reissi* (Lauraceae), *Persea coriacea* (Lauraceae), *Phorodendron fossile* (Loranthaceae), *Pisonia witti* (Nyctaginaceae), *Pithecolobium ecuadorensis*, *P. presaman* (Leguminosae), *Plumeria tertiaria* (Apocynaceae), *Posoqueria columbiana* (Rubiaceae), ?*Pterogyne oblongifolium* (Leguminosae), *Rhamnidium elaeocarpoides* (Rhamnaceae), *Ruprechtia braunii* (Polygonaceae), *Serjania tertiaria* (Sapindaceae), *Sparattanthelium pliocenicum* (Hernandiaceae), *Stenolobium rhomboidalis* (Leguminosae), *Styrax styracioides* (Styracaceae), *Talisia ecuadoriana* (Sapindaceae), *Tapiria lanceolata* (Anacardiaceae), *Tetracera tertiaria* (Dilleniaceae), *Trichilia hirtaformis* (Meliaceae), *Trigonia varians* (Trigoniaceae), *Vochysia ferruginoides* (Vochysiaceae). Incertae sedis: *Phyllites celastrinoides*, *P. gouareoides* (see also *Loxopterygium laplayense* [Anacardiaceae] and *Tipuana ecuatoriana* [Leguminosae] from the Azogues Formation [Miocene], Valley of Cuenca; Burnham & Carranco [2004] and Burnham [1995])

[31, Loja, Tablayacu, formation?, Mio–Pliocene]

Loja—Fungi: *Hysterites ellipticus*, *Sphaerites consociatus*, *S. punctiformis*, *S. sparsus*, *Xylomites immersus*. Angiosperms (monocotyledons): *Poacites magnus* (Gramineae), *Scleria wolfi* (Cyperaceae). Angiosperms (dicotyledons): *Arthante geniculatoides* (Piperaceae), *Banisteria aceroides* (Malpighiaceae), *Bombax retusifolium* ([Bombacaceae], Malvaceae original author), *Caesalpinia subdimidiata* (Leguminosae), *Camphoromoea speciosa* (Lauraceae), *Cassia dimidiato-linearis*, *C. linearifolia*, *C. longifolia* (Leguminosae), *Endlicheria rhamnoides* (Rubiaceae), *Eugenia ovalifolia* (Myrtaceae), *Hieronymia lehmanni* (Euphorbiaceae), *Hiraea cyclosperma* (Malpighiaceae), *Inga latifolia*, *I. ovalifolia* (Leguminosae), *Leguminosites acaciaeformis*, *L. cassioides*, *L. grandis*, *L. machaerioides*, *Lonchocarpus obtusifolius* (Leguminosae), *Luhea tertiaria* (Tiliaceae), *Macrolobium tenuifolium* (Leguminosae), *Myrcia antediluviana* (Myrtaceae), *Myrciaria tenuifolia* (Myrtaceae), *Myristica fossilis* (Myristicaceae), *Phoradendron fossile* (Loranthaceae), *Pterogyne oblongifolia* (Leguminosae), *Stenolobium rhomboidalis* (Leguminosae), *Tapiria lanceolata* (Anacardiaceae), *Vochysia ferruginoides*, *V. witti* (Vochysiaceae). Incertae sedis: *Phyllites celastrinoides*, *P. colubrinoides*, *P. gouareoides*, *P. styracioides*

Tablayacu—Angiosperm (monocotyledon): *Poacites magnus* (Gramineae). Angiosperms (dicotyledons): *Cassia longifolia* (Leguminosae), *Couratari tertiaria* (Lecythidaceae)

Colombia

Megafossils

[32, Santa Ana (Río Magdalena), Cáucathales, formation? Mio–Pliocene]

Santa Ana—Angiosperms (monocotyledons): *Bambusium stubeli* (Gramineae), *Musophyllum elegans* (Musaceae), *Rhizoma graminis* (Gramineae), *Stenospermatium columbiense* (Araceae). Angiosperms (dicotyledons): *Acrodiclidium chartaceum* (Lauraceae), *Bothriospora witti* (Rubiaceae), *Bu(y)ttneria cinnamomifolia* (Sterculiaceae), *Chrysophyllum rufoides* (Sapotaceae), *Citharexylon retiformis* (Verbenaceae), *Condaminea grandifolia* (Rutaceae), *Ficus laqueata* (Moraceae), *Goppertia subherbacea* (Lauraceae), *Gouiana firma*, *G. membranacea* (Rhamnaceae), *Ilex arcinervis* (Aquifoliaceae), *Inga reissi* (Leguminosae), *Jambosa lanceolata* (Myrtaceae), *Laurophyllum rigidum* (Lauraceae), *Moquillea stubeli* (Rosaceae, Chrysobalanaceae), *Moschoxylon tenuinerve* (Meliaceae), *Nectandra areolata*, *N. curvatifolia*, *N. reissi* (Lauraceae), *Persea coriacea*, *P. elliptica*, *P. elongata*, *P. macrophylloides* (Lauraceae), *Pithecolobium tenuifolium* (Leguminosae), *Styrax lanceolata* (Styracaceae), *Tecoma grandidentata* (Bignoniaceae), *Trigonia varians* (Trigoniaceae), *Vochysia retusifolia* (Vochysiaceae). Incertae sedis: *Phyllites abutoides*, *P. strychnoides*, *P. vochysioides*. Cáucathales—Ferns and allied groups: *Meniscium* [*Thelypteris*] *wolfi* (Thelypteridaceae), *Salvinia lechmanni* (Salviniaceae). Angiosperm (monocotyledon): *Palmacites* (Palmae). Angiosperms (dicotyledons): *Posoqueria columbiana* (Rubiaceae), *Sabicea asperifolia* (Rubiaceae)

[33, Magdalena Valley, Department of Santander, ~350 mi. inland from the Caribbean coast, formation?, Miocene]

Angiosperms (monocotyledons): *Dioscorea* (Dioscoreaceae), *Palmophyllum* (Palmae). Angiosperms (dicotyledons): *An(n)ona* cf. *guppyi* (Annonaceae), *Avicennia miocenica* (Verbenaceae), *Bue(y)ttineria* (Sterculiaceae), *Couroupita santanderensis* (Lecythidaceae), *Coussapoa* (Moraceae), *Eugenia comparabilis* (Myrtaceae), *Ficus* cf. *betijoquensis*, *F. talamancana* (Moraceae), *Hernandia tongi* (Hernandiaceae), *Mespilodaphne colombiana* (Lauraceae), *Persea coriacea* (Lauraceae), *Posoqueria columbiana* (Rubiaceae), *Rheedia miocenica* (Guttiferae, Clusiaceae), *Tapirira lanceolata* (Anacardiaceae). Incertae sedis: *Phyllites*

[34, Río Casanare (west of Salina), Río Tablona, Zamaricote (near Río Tablona), formation?, Mio–Pliocene]

Ferns and allied groups: *Goniopteris* [*Thelypteris*] *cochabambensis* (Thelypteridaceae). Angiosperms (dicotyledons): *Bignonia tertiaria* (Bignoniaceae), *Cassia aguayensis*, *C. zuliana* (Leguminosae), *Ficus betijoquensis* (Moraceae), *Inga lojana*, *I. reissi* (Leguminosae), *Leguminosites casareana* (Leguminosae), *Mespilodaphne acrensis* (Lauraceae), *Pithecolobium* [*Pithecellobium*] *presaman* (Leguminosae), *Rheedia* (Guttiferae, Clusiaceae), *Sparattanthelium pliocenicum* (Hernandiaceae), *Triptolemaea tertiaria* (Leguminosae)

[35, Río Cauca, Department of Antioquia, formation?, Late Tertiary; see also Pons, 1984, listed as Antioquia Formation, late Oligocene]

Angiosperms (dicotyledons): *Anacardioxylon caracoli* (Anacardiaceae), *Goupioxylon stutzeri* (Goupiaceae), *Guttiferoxylon compactum*, *G. platonioides* (Guttiferae, Clusiaceae), *Leguminoxylon grossei* (Leguminosae), *Sapindoxylon antioquiense* (Sapindaceae), *Terminalioxylon naranjo*, *T. porosum* (Combretaceae)

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. *(Continued)*

[36, Department of Tolima, Mesa Formation, Late Tertiary, included under Pliocene in Appendix 2]

Ferns and allied groups: *Cyathea colombiensis* (Cyatheaceae). Angiosperms (monocotyledons): *Heliconiophyllum elegans*, *H. falanense* (Heliconiaceae). Angiosperms (dicotyledons): *Calophyllites mesaensis* (Guttiferae, Clusiaceae), *Coussapoites portae*, *C.* aff. *veracruziana* (Moraceae), *Muntingiophyllum calaburoides* (Elaeocarpaceae). Summary of plants mentioned in Pons (1985) for localities at Falan, Hato Grande, Penagos, and Lumbi in the Mesa Formation: Angiosperms (monocotyledons): *Bambusium stubeli* (Gramineae), *Heliconiophyllum falanense* (Heliconiaceae), *Rhizoma graminis* (Gramineae), *Stenospermatium columbiense* (Araceae). Angiosperms (dicotyledons): *Acrodiclidium chartaceum* (Lauraceae), *Bothriospora witti* (Rubiaceae), *Buettneria cinnamomifolia* (Sterculiaceae), *Calophyllites mesaensis* (Guttiferae, Clusiaceae), *Chrysophyllum rufoides* (Sapotaceae), *Citharexylon retiforme*(*mis*) (Verbenaceae), *Condaminea grandifolia* (Rutaceae), *Ficus laqueata* (Moraceae), *Goeppertia subherbacea* (Lauraceae), *Gouania firma*, *G. membranacea* (Rhamnaceae), *Ilex arcinervis* (Aquifoliaceae), *Inga reissi* (Leguminosae), *Jambosa lanceolata* (Myrtaceae), *Moquilea stubeli* (Rosaceae), *Moschoxylon tenuinerve* (Meliaceae), *Nectandra areolata*, *N. curvatifolia*, *N. reissi* (Lauraceae), *Ocotea* cf. *rubra* (Lauraceae), *Persea coriacea*, *P. elliptica*, *P. elongata*, *P. macrophylloides* (Lauraceae), *Pithecolobium tenuifolium* (Leguminosae), *Styrax lanceolata* (Styracaceae), *Tecoma grandidentata* (Bignoniaceae), *Trigonia varians* (Trigoniaceae), *Vochysia retusifolia* (Vochysiaceae). Incertae sedis: *Phyllites abutoides*, *P. strychnoides*, *P. vochysioides*

[37, Upper and Middle Magdalena Valley, Honda Group (Tertiary); Sincelejo–Ovejas, Department of Bolívar, formation?, Miocene]

Angiosperm (dicotyledon): *Goupioxylon stutzeri* (Goupiaceae)

[38, Toluviejo–Corozal region, Department of Sucre, Corozal Formation, Late Tertiary, included under Pliocene in Appendix 2]

Angiosperm (dicotyledon): *Crudioxylon pinalense*, *C.* sp. (Leguminosae)

[39, High Plain of Bogotá and vicinity, Neogene, included under Pliocene in Appendix 2; based on "Atlas of Neogene plant fossils from the High Plain of Bogotá and surroundings (Eastern Cordillera, Colombia)," Wijninga, 1996a (Ref. 39; see also Tables 4.1, 5.1, 6.1, 6.2, 7.1, 7.3; Appendices 1, 2); unidentified not included]

Microfossils

Fungi: *Hiospira*, *Microthyrium*, *Neurospora*. Algae: cf. *Spirogyra*. Ferns and allied groups: *Crassoretitriletes vanraadshoovenii* (Schizaeaceae, *Lygodium*), *Danaea* (Marattiaceae). Angiosperms (monocotyledons): *Anthurium* (Araceae), *Astrocaryum* (Palmae), cf. *Catopsis* (Bromeliaceae), *Retimonocolpites retifossulatus* (Palmae). Angiosperms (dicotyledons): *Brownea* (Leguminosae), cf. Chrysobalanaceae, cf. *Connarus* (Connaraceae), *Ecclinusa* (Sapotaceae), *Humiriastrum* (Humiriaceae), cf. *Machaerium* (Leguminosae), cf. *Macoubea* (Apocynaceae), *Paraprotium* (Burseraceae), cf. *Psychotria* (Rubiaceae), *Rheedia* (Guttiferae, Clusiaceae), cf. Rubiaceae

Megafossils

Bryophyta: Hepaticeae, aff. *Lejeunea*, aff. *Prionolejeunea*. Musci: aff. *Breutelia*, aff. Hookeriaceae, *Sphagnum* (Sphagnaceae), aff. Thuidiaceae. Ferns and allied groups: *Azolla* (Salviniaceae), Polypodiales, *Selaginella* (Selaginellaceae). Gymnosperms: *Decussocarpus* (Podocarpaceae), *Podocarpus* (Podocarpaceae). Angiosperms (monocotyledons): Alismataceae, cf. *Asplundia* (Cyclanthaceae), *Carex* (Cyperaceae), cf. *Cyclanthus* (Cyclanthaceae), *Eleocharis* (Cyperaceae), cf. *Evodianthus* (Cyclanthaceae), *Juncus* (Juncaceae), Palmae, cf. *Scirpus* (Cyperaceae), *Thoracocarpus* (Cyclanthaceae), *Xyris* (Xyridaceae). Angiosperms (dicotyledons): cf. *Anacardium* (Anacardiaceae), *Callitriche* (Callitrichaceae), *Cecropia* (Urticaceae–Moraceae), Compositae, *Coussapoa* (Urticaceae–Moraceae), *Elatine* (Elatinaceae), *Freziera* (Theaceae), *Gunnera* (Haloragidaceae [Gunneraceae]), *Hippocratea–Pristimera* (Celastraceae), *Humiriastrum* (Humiriaceae), *Ludwigia* (Onagraceae), Lythraceae, Melastomataceae, Nymphaeaceae, *Parinari* (Chrysobalanaceae), cf. *Polygonum* (Polygonaceae), *Pristimera* (see *Hippocratea/Pristimera*), *Ranunculus* (Ranunculaceae), *Rubus* (Rosaceae), *Sacoglottis*, *S. tertiaria* (Humiriaceae), Solanaceae, *Symplocos* (Symplocaceae), *Turpinia* (Staphyleaceae), *Urtica* (Urticaceae), *Vantanea* (Humiriaceae), *Zanthoxylum* (Rutaceae)

Venezuela

Miocene

Megafossils

[40, Betijoque, state of Trujillo, formation?, middle to late Miocene]

Ferns and allied groups: *Blechnum betijoquensis* (Blechnaceae). Angiosperms (monocotyledons): *Heliconia elegans* (Heliconiaceae), *Sabalites* (Palmae). Angiosperms (dicotyledons): *Anona guppyi* (Annonaceae), *Antholithus venezuelensis* (Symplocaceae), *Apocynophyllum salvadorensis* (Apocynaceae), *Burserites venezuelana* (Burseraceae), *Coussapoa villosoides* (Urticaceae), *Ficus betijoquensis* (Moraceae), *Leguminosites entadaformis*, *L. venezuelensis* (Leguminosae), *Rhizophora boweni* (Rhizophoraceae), *Simarouba miocenica* (Simaroubaceae), *Sophora salvadorana* (Leguminosae), *Trigonia varians* (Trigoniaceae)

[41, Cuque, Cumbarebo oil field, state of Falcón, Damsite series, late Miocene]

Angiosperm (monocotyledon): *Caladiosoma miocenica* (Araceae). Angiosperms (dicotyledons): *Anacardites americanus* (Anacardiaceae), *Colubrina miocenica* (Rhamnaceae), *Gyrocarpus miocenica* (Hernandiaceae), *Leguminosites cuquensis* (Leguminosae), *Melloa* (?) *cuquensis* (Bignoniaceae), *Mimosites suteri* (Leguminosae), *Sideroxylon mastichodendroides* (Sapotaceae)

[42, Quebrada Chiquero, Pariaguán, state of Anzoátegui, formation?, Pliocene]

Angiosperms (dicotyledons): *An(n)ona saraviana* (Annonaceae), *Calophyllum calabaformis* (Guttiferae, Clusiaceae), *Cassia leptocarpoides* (Leguminosae), *Cedrela preodorata* (Meliaceae), *Chrysophyllum cainitoformis* (Sapotaceae), *Combretum jacquinifolia* (Combretaceae), *Eugenia camparabilis* (Myrtaceae), *Geissanthus brittoni* (Myrsinaceae), *Hernandia* (Hernandiaceae), *Inga kugleri* (Leguminosae), *Maytenus anzoateguiensis*, *M. trinitense* (Celastraceae), *Mimusops miocenica* (Sapotaceae), *Nectandra curvatifolia* (Lauraceae), *Persea macrophylloides*, *P. preamericana* (Lauraceae), *Pithecolobium tenuifolium* (Leguminosae), *Rheedia preacuminata* (Guttiferae), *Styrax lehneri* (Styracaceae), *Tapirira lanceolata* (Anacardiaceae), *Theobroma tertiaria* (Sterculiaceae), *Trichilia hirtaformis* (Meliaceae), *Trigonia varians* (Trigoniaceae)

Microfossils

[43, Maracaibo, Falcón, and Eastern basins, various formations, Oligocene–[Miocene]–Pleistocene]

Algae: *Botryococcus*, *Mougeotia*, *Pediastrum*. Ferns and allied groups: *Azolla* (Salviniaceae), triletes—*Cicatricosisporites baculatus* (Schizaeaceae, *Anemia*), *C. dorogensis* (Schizaeaceae), *Cingulatisporites*, *Crassoretitriletes vanraadshooveni* (Schizaeaceae, *Lygodium*), *Cyatheacidites annulatus* (Lophosoriaceae, *Lophosoria*), *Deltoidospora adriennis* (Pteridaceae, *Acrostichum*), *Echitriletes muelleri*, *Foveotriletes margaritae*, *F. ornatus* (cf. Lycopodiaceae, *Lycopodium*), *Kuylisporites waterbolki* (Cyatheaceae, *Cnemidaria*), *Magnastriatites grandiosus* (Pteridaceae, *Ceratopteris*), *Nijssenosporites fossulatus* (Pteridaceae, *Pityrogramma*), *Polypodiaceoisporites pseudopsilatus* (Pteridaceae, *Pteris*), *P.* cf. *speciosus* (cf. Lycopodiaceae, *Lycopodium*), *Retitriletes sommeri*, *Verrucatotriletes* cf. *bullatus*, monoletes—*Echinosporis*, *Laevigatosporites catanejensis*, *L. vulgaris*, *Perinomonoletes*, *Verrucatosporites* cf. *speciosus*, *V. usmensis*. Angiosperms (?): *Clavainaperturites clavatus*, *Grimsdalea magnaclavata*. Gymnosperm: *Podocarpidites* (Podocarpaceae). Angiosperms (monocotyledons): *Clavamonocolpites lorentei* (Palmae?), *Cyperaceaepollis* cf. *neogenicus* (Cyperaceae), *Echidiporites barbeitoensis* (Palmae, *Korthalsia* [Indomalaysia]), *Longapertites vaneendenburgi* (Palmae?), *Mauritiidites franciscoi* (Palmae, *Mauritia*), *Monoporites annulatus* (Gramineae), *Orchideamasulites schlecteri* (Orchidaceae; see Di Giacomo, 1985), *Proxapertites cursus*, *P. minutus* (Palmae, cf. *Astrocaryum*), *P. operculatus* (Palmae, cf. *Astrocaryum*), *P. tertiaria* (probably Annonaceae), *Psilamonocolpites medius* (Palmae), *Retimonocolpites longicolpatus* (Palmae?), *R. retifossulatus* (Palmae), *Spinozonocolpites echinatus* (cf. *Nypa*, but here redeposited), *Trichotomocolpites*. Angiosperms (dicotyledons): *Alnipollenites verus* (Betulaceae, *Alnus*), *Anacolosidites* cf. *luteoides*, *Bombacacidites baculatus* (Bombacaceae, *Pachira*), *B. baumfalki*, *B. bellus*, *B. ciriloensis*, *B. zuatensis* (Bombacaceae), *Clavatricolporites* cf. *leticiae*, *Corsinipollenites oculusnoctis* (Onagraceae), *Crassiectoapertites columbianus*, *Crototricolpites annemariae*,

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. *(Continued)*

Echiperiporites estelae (Malvaceae), *Echitricolporites maristellae*, *E. mcneillyi* (Compositae), *E. spinosus* (Compositae), *Echitriporites trianguliformis*, *Ericipites* (Ericaceae), *Fenestrites longispinosus*, *F. spinosus* (Compositae), *Ilexpollenites iliacus*, *I. margaritatus* (Aquifoliaceae, *Ilex*), *Jandufouria seamrogiformis* (Bombacaceae, *Catostemma*), *Magnaperiporites spinosus*, *Malvacipollis spinulosa* (cf. Euphorbiaceae), *Maravenites polyoratus*, *Margocolporites vanwijhei* (Leguminosae, cf. *Caesalpinia*), *Momipites*, *Multiareolites formosus* (Acanthaceae), *Multimarginites vanderhammeni* (Acanthaceae), *Myrtaceidites* (Myrtaceae), *Pachydermites diederixi* (Guttiferae, *Symphonia*), *Perfotricolpites digitatus* (Convolvulaceae), *Perisyncolporites pokornyi* (Malpighiaceae), *Polyadopollenites mariae* (Leguminosae, cf. *Acacia*), *Proteacidites dehaani*, *P. triangulatus* (Proteaceae), *Psiladiporites minimus* (Moraceae), *Psilaperiporites minimus*, *P. robustus* (Chenopodiaceae–Amaranthaceae), *Psilastephanocolporites fissilis* (Polygalaceae), *Psilastephanoporites stellatus*, *Psilatricolporites caribbiensis*, *P. crassus* (Pelliceriaceae, *Pelliceria*), *P. devriesi*[*i*] (Humiriaceae, *Humiria*), *P. divisus*, *P. maculosus* (Sapotaceae, cf. *Chrysophyllum*), *P. operculatus* (Euphorbiaceae, *Alchornea*), *P. pachydermatus*, *P. transversalis* (Sapotaceae), *P. triangularis*, *P. venezuelanus*, *Retibrevitricolpites* cf. *catatumbus*, R. *triangulatus*, *Retistephanoporites crassiannulatus* (Bombacaceae), *Retitricolpites amapaensis*, R. *simplex*, *Retitricolporites* (Verbenaceae, *Avicennia*), R. cf. *amazonensis*, R. cf. *brevis*, R. *guianensis* (cf. Sterculiaceae), R. *hispidus*, R. *irregularis* (Euphorbiaceae, cf. *Amanoa*), *Scabratricolporites planetensis*, *Stephanocolpites evansii*, *Striatricolpites catatumbus* (Leguminosae, cf. *Crudia* type), *Striatricolporites tenuissimus*, *Venezuelites globoannulatus* (Mendociaceae?), *Verrutricolporites rotundiporus* (Lythraceae, *Crenea*), *Zonocostites ramonae* (Rhizophoraceae, *Rhizophora*)

Trinidad

Miocene

Megafossils

[44, Trinidad, Forest Sand and porcellanite beds, Siparia, formation?, Miocene; see also Berry, 1925f, 1937g, h]

Angiosperms (monocotyledons): *Caladiosoma miocenica* (Araceae), *Costus* (?) *incertus* (Zingiberaceae), *Heliconia elegans* (Heliconiaceae), *Palmocarpon bactrioides*, *P. fusiforme*, *Palmophyllum* (Palmae). Angiosperms (dicotyledons): *Anacardites americanus*, *A. spondiaeformis* (Anacardiaceae), *Bombax prebarrigon* (Bombacaceae), *Brosimum miocenicum* (Moraceae), *Bumelia trinitense* (Sapotaceae), *Calophyllum calabaformis* (Guttiferae), *Canavalia miocenica* (Leguminosae), *Cassia kugleri*, *C. leptocarpoides*, *C. longifolia*, *C. sipariensis*, *C. zuliana* (Leguminosae), *Cedrela preodorata*, *C.* (?) *tertiaria* (Meliaceae), *Clusia vera* (Guttiferae), *Colubrina miocenica* (Rhamnaceae), *Combretum incertum* (Combretaceae), *Coussapoa vaningeni* (Moraceae), *Echites ettingshauseni* (Apocynaceae), *Eugenia comparabilis* (Myrtaceae), *Fagara miocenica* (Rutaceae), *Ficus porcellanaria* (Moraceae), *Inga kugleri* (Leguminosae), *Lecythidoanthus kugleri* (Lecythidaceae), *Leguminosites canavaliformis*, *L. silvensis*, *L. trinitensis* (Leguminosae), *Maytenus trinitense* (Celastraceae), *Mimusops anomala*, *M. miocenica* (Sapotaceae), *Nectandra curvatifolia*, *N. kugleri*, *N. silvarenaria* (Lauraceae), *Persea macrophylloides*, *P. preamericana* (Lauraceae), *Piperites* cf. *cordatus* (Piperaceae), *Pithecolobium tenuifolium* (Leguminosae), *Plumiera alia* (Apocynaceae), *Rhamnidium miocenicum* (Rhamnaceae), *Rheedia miocenica* (Guttiferae), *Sideroxylon mastichodendroides* (Sapotaceae), *Styrax* (?) *lehneri* (Styracaceae), *Tapirira trinitiana* (Anacardiaceae), *Terminalia trinitense* (Combretaceae), *Trichilia hirtaformis* (Meliaceae)

Microfossils

[45, Pitch Lake, 1 mi. S of Brighton, Forest/Cruse Series, Miocene; generic identifications only, generic affinities uncertain, approximate family affiliations]

Fungi: *Circulisporites*, *Diporisporites*, *Lacrimasporonites*. Ferns and allied groups: *Cyathidites* (Cyatheaceae), *Intrapunctatisporites*, *Matonisporites* (Matoniaceae), *Osmundacidites* (Osmundaceae), *Polypodiaceaesporites*, *Verrucatosporites*. Gymnosperm: *Podocarpidites* (Podocarpaceae). Angiosperms (monocotyledons): *Arecipites* (Palmae), *Liliacidites* (Liliaceae), *Monoporopollenites* (Gramineae), *Monosulcites* (Palmae), *Palmaepollenites* (Palmae). Angiosperms (dicotyledons): *Compositoipollenites* (Compositae), *Cupuliferoidaepollenites* (Fagaceae), *Cyrillaceaepollenites* (Cyrillaceae), *Engelhardtiopollenites* (Juglandaceae), *Ilexpollenites* (Aquifoliaceae), *Myricipites* (Myricaceae), *Polycolpites* (Fagaceae), *Polygalacidites* (Polygalaceae), *Psiladiporites* (Moraceae), *Psilasyncolporites* (Myrtaceae), *Psilatricolporites* (Euphorbiaceae), *Quercoidites* (Tiliaceae), *Retitricolpites* (Cruciferae), *Rhoipites* (Anacardiaceae), *Sapotaccoidaepollenites* (Sapotaceae), *Tetrapollis* (Ulmaceae), *Verrutricolporites* (?Lythraceae)

Brazil

Pliocene

Megafossils

[46, Aramarý, state of Bahia (105 km N of city of Bahia), formation?, Pliocene]

Fungi: *Caenomyces braziliensis*. Ferns and allied groups: *Hemitelia branneri*. Angiosperms (dicotyledons): *Anacardites braz(s)iliensis* (Anacardiaceae), *Bombax aramariensis* (Bombacaceae), *Bumelia cuneatoides*, *B. marahiana* (Sapotaceae), *Calyptranthes marahiensis* (Myrtaceae), *Canella winterianafolia* (Canellaceae), *Cassia marahiana* (Leguminosae), *Chrysobalanus precuspidatus*, *C. preicaco* (Rosaceae), *Cinnamomum incertum* (Lauraceae), *Citrophyllum bahiensis* (Rosaceae), *Coccolobis tertiaria* (Polygonaceae), *Couroupita ovata* (Lecythidaceae), *Dalbergia ettingshauseni* (Leguminosae), *Dodonaea vera* (Sapindaceae), *Erythrochiton bahiense* (Rutaceae), *Fagara dentatafolia*, *F. formosa* (Rutaceae), *Ficus aramaryensis*, *F. mamilliferafolia* (Moraceae), *Guaiacum pliocenicum* (Zygophyllaceae), *Gyminda latifolioides* (Celastraceae), *Huberia preovalifolia* (Melastomataceae), *Ilex bahiana* (Aquifoliaceae), *Inga myrianthafolia* (Leguminosae), *Jacaranda tertiaria* (Bignoniaceae; see Berry, 1933), *Kielmeyera tertiaria* (Guttiferae), *Leguminosites bahiensis*, *L. braziliensis*, *L. hymenaeoides*, *L. machaerioides* (Leguminosae), *Leptolobium eonitens* (Leguminosae), *Maytenus dasycladoides* (Celastraceae), *Miconia ettingshauseni*, *M. prealbicans* (Melastomataceae), *Myrcia rostrataformis* (Myrtaceae), *Myrsine ciliatafolia* (Myrsinaceae), *Pilocarpus prepinnatifolius* (Rosaceae), *Pisonia branneri* (Nyctaginaceae), *Plumeria rubraformis* (Apocynaceae), *Psidium cuneatifolium* (Myrtaceae), *Rheedia pliocenica* (Guttiferae), *Rollinia tertiaria* (Annonaceae), *Sapindus presaponaria* (Sapindaceae), *Simaruba whitei* (Simarubaceae), *Spondias mirifica* (Anacardiaceae), *Styrax preferrugineum* (Styracaceae), *Trichilia branneri* (Meliaceae), *Vochysia acuminatafolia* (Vochysiaceae). Incertae sedis: *Antholithes bahiana*, *A. kielmeyerana*, *Carpolithus badieroides*, *C. bahiensis*, *Phyllites bahiana*, *P. marahiensis*

[47, Mocambo (Bahia, = Aramarý site of Ref. 24 above), Fonseca (Minas Gerais), formation (?), Pliocene]

Angiosperm (monocotyledon): *Heliconia bahiana* (Heliconiaceae). Angiosperms (dicotyledons): *Arrabidaea* (Bignoniaceae), *Banisteria oblongifolia* (Malpighiaceae), *Caesalpinia echinataformis* (Leguminosae), *Cassia fonsecana*, *C. obtusatafolia* (Leguminosae), *Cedrela campbeli* (Meliaceae), *Coccolobis preuvifera* (Polygonaceae), *Combretum fonsecanensis* (Combretaceae), *Erythrochiton bahiense* (Rutaceae), *Homalanthus prenutans* (Euphorbiaceae), *Jacaranda tertiaria* (Bignoniaceae), *Labatia fonsecana* (Sapotaceae), *Myrsine braziliana* (Myrsinaceae), *Sapindus presaponaria* (Sapindaceae), *Siparuna preguayensis* (Monimiaceae), *Terminalia maxima* (Combretaceae), *Triptolema(c)ea tertiaria* (Leguminosae)

[48, Fonseca, Minas Gerais, formation(?), Pliocene]

Angiosperms (dicotyledons): *Tibouchina dolianitii*, *T. santosii* (Melastomataceae)

[49, Fonseca, Minas Gerais, formation (?), Pliocene]

Angiosperms (dicotyledons): *Annona carnavalii*, *A. lamegoi*, *A. oliveirae* (Annonaceae), *Oxandra emygdiana* (Annonaceae)

Miocene

Microfossils (including related deposits in Colombia)

[50, Solimões Basin (Brazil), Caquetá River (Colombia), lower Apaporis River (Colombia), Solimões–Pebas formations, early to late Miocene; some references to genus are apparently meant only to indicate a similar morphological type]

Fungi: *Tetraploa* cf. *aristata*. Algae: *Botryococcus*, *Pediastrum*. Ferns and allied groups: *Bacutriletes* (Selaginellaceae, *Selaginella*), *Clavatriletes*, *Crassoretitriletes vanraadshoovenii*

Table 7.2. Plant fossils from the Neogene (Miocene and Pliocene) of South America. *(Continued)*

(Schizaeaceae, *Lygodium*), *Cyatheacidites* (Cyatheaceae), *Deltoidospora adriennis* (Pteridaceae, *Acrostichum*), *Echinosporis*, *Echitriletes* cf. *muelleri*, *Foveotriletes ornatus* (Lycopodiaceae), *Kuylisporites waterbolki* (Cyatheaceae, *Cyathea*), *Laevigatosporites catanejensis* (Blechnaceae, *Blechnum* [type]), *Magnastriatites grandiosus* (Pteridaceae, *Ceratopteris*), *Matonisporites mulleri*, *Perinomonoletes*, *Polypodiaceoisporites*, *Psilamonoletes tibui*, *Psilatriletes* sp. 1 (Vittariaceae, *Polytaenium*), *P.* sp. 2 (Schizaeaceae, *Lygodium*), *P. lobatus*, *P. peruanus* (Pteridaceae, *Pteris*), *Rugotriletes*, *Verrucatosporites usmensis*, *Verrucatotriletes* cf. *bullatus* (Cyatheaceae, *Alsophila*), *Verrutriletes*. Gymnosperm: *Podocarpidites* (Podocarpaceae, *Podocarpus*). Angiosperms (monocotyledons): *Clavamonocolpites* (Palmae, *Iriartea*), *Cyperaceaepollis* (Cyperaceae), *Echidiporites barbeitoensis* (Palmae), *Echimonocolpites*, *Ephedripites renzonii* (Araceae, *Spathiphyllum*), *Grimsdalea magnaclavata*, *Mauritidites franciscoi* (Palmae, *Mauritia*), *Monoporites annulatus* (Gramineae), *Psilamonocolpites amazonicus* (Palmae, *Euterpe*), *P. nanus*, *P. rinconii* (Palmae), *Retimonocolpites absyae*, *R. longicolpatus*, *R. maximus*, *R. retifossulatus* (Palmae), *Trichotomosulcites* (Palmae, *Bactris*). Angiosperms (dicotyledons): *Bombacacidites araracuarensis* (Bombacaceae, *Ceiba*), *B. baculatus* (Bombacaceae, *Pachira*), *B. baumfalkii* (Bombacaceae), *B. bellus* (Bombacaceae, *Bombax*), *B. muinaneorum* (Bombacaceae, *Bombacopsis*), *Clavainaperturites microclavatus* (Chloranthaceae, *Hedyosmum*), *Corsinipollenites oculusnoctis* (Onagraceae, *Ludwigia*), *Crassiectoapertites columbianus* (Leguminosae), *Cricotriporites guianensis*, *Crototricolpites annemariae* (Euphorbiaceae, *Croton* [type]), *Echiperiporites akanthos*, *E. estelae*, *Echitricolporites maristellae*, *Heterocolpites incomptus* (Melastomataceae, cf. *Miconia*), *H. rotundus*, *H. verrucosus* (Melastomataceae), *Ilexpollenites* (Aquifoliaceae, *Ilex*), *Jandufouria seamrogiformis* (Bombacaceae, *Catostemma*), *Magnaperiporites spinosus*, *Margocolporites vanwijhei* (Leguminosae, cf. *Caesalpinia*), *Multimarginites vanderhammenii* (Acanthaceae), *Perfotricolpites digitatus* (Convolvulaceae, *Merremia* [type]), *Perisyncolporites pokornyi* (Malpighiaceae), *Polyadopollenites* (Leguminosae, cf. *Inga*), *P. mariae* (Leguminosae, *Acacia*), *Proteacidites* cf. *triangulatus*, *Proxapertites tertiaria* (Annonaceae, *Crematosperma*), *Psiladiporites minimus* (Moraceae), *P. redundantis* (Moraceae), *Psilaperiporites minimus* (Amaranthaceae–Chenopodiaceae), *P. multiporus*, *Psilastephanocolporites fissilis* (Polygalaceae), *P. marinamensis* (Sapotaceae), *P. matapiorum*, *P. schneideri*, *Psilastephanoporites herngreenii* (Apocynaceae), *Psilatricolpites acerbus*, *P. anconis*, *P. minutus*, *P.* cf. *papilioniformis*, *P. pulcher*, *P. simplex*, *Psilatricolporites atalayensis*, *P. costatus*, *P. crassus* (Pelliceraceae, *Pelliceria*), *P. cyamus*, *P. devriesii* (Humiriaceae, *Humiria*), *P. divisus* (Sapotaceae), *P. exiguus*, *P. garzonii*, *P. labiatus* (Sapotaceae, *Pouteria*), *P. magniporatus*, *P. obesus*, *P. operculatus* (Euphorbiaceae, *Alchornea*), *P. silvaticus*, *P. triangularis*, *P.* cf. *varius*, *P. venezuelanus*, *Psilatriporites corstanjei* (Rubiaceae, *Faramea* [?]), *P. desilvae* (Leguminosae, Caesalpinioideae), *P. sarmientoi*, *Retibrevitricolpites catatumbus*, *R. yavarensis*, *Retimonocolpites absyae* (Myristicaceae, *Virola*), *Retistephanoporites angelicus*, *R. crassiannulatus* (Bombacaceae, *Quararibaea*), *Retitricolpites amapaensis*, *R. antonii*, *R. caquetanus*, *R. colpiconstrictus*, *R. depressus*, *R. lalongatus*, *R. lewisii*, *R. lorenteae* (Bombacaceae, *Bombax*), *R.* cf. *maledictus*, *R.* cf. *maturus*, *R. simplex*, *R. tuberosus*, *R. wijningae*, *Retitricolporites caputoi*, *R. crassicostatus* (Rubiaceae), *R. crassopolaris*, *R. ellipticus*, *R. guianensis*, *R. hispidus*, *R. irregularis* (Euphorbiaceae, *Amanoa*), *R. kaarsii* (Euphorbiaceae, *Dalechampia*), *R. latus*, *R. leticianus*, *R. medius*, *R. milnei*, *R. oblatus*, *R. poriconspectus* (Leguminosae), *R. pygmaeus*, *R. santaisabelensis*, *R. solimoensis*, *R. ticuneorum*, *R. wijmstrae*, *Retitriporites dubiosus*, *Rugutricolporites arcus* (Chrysobalanaceae, *Licania*), *Scabratriporites redundans*, *Spirosyncolpites spiralis*, *Stephanocolpites evansii*, *Striatricolpites catatumbus* (Leguminosae, *Crudia* type), *Syncolporites anibalii* (Sapindaceae), *S.* cf. *incomptus*, *S. poricostatus* (Myrtaceae), *Verrutricolporites rotundiporus* (Rhizophoraceae, *Rhizophora*), *Zonocostites duquei* (Rhizophoraceae, *Rhizophora*)

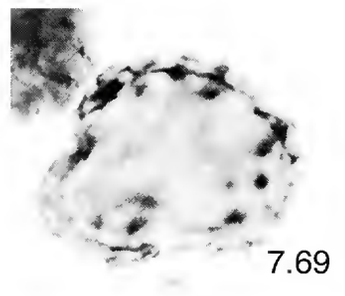
NEOGENE (MIOCENE AND PLIOCENE), 23.8–2.6 MA

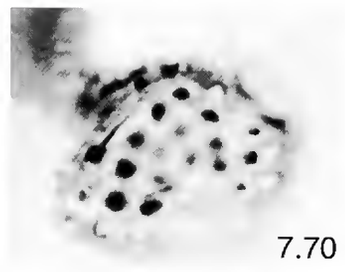
The paleobotanical database for the Neogene of southern South America is not extensive, but global trends in climate, well-established tectonic configurations, stratigraphic ranges of lineages and individual taxa, and the sequence of appearance of vegetation types, as well as local orogenic history, provide provenance for identifications and interpretations. By the beginning of the Miocene (23.8 Ma), the thermal isolation of Antarctica had long been completed by the opening of the Drake Passage and formation of the circum-Antarctic Current (~34 Ma). Continental glaciations were under way and the Humboldt Current was in operation (~30 Ma). Climates were becoming more seasonal with increasing amounts of cold water entering the world's oceans. A continuing decline in the rate of plate movement reduced atmospheric CO_2 concentration, and the long-operating Milankovitch variations became increasingly more evident in driving climates into the icehouse interval and toward the Ice Age. The connection between South America and Australia via Antarctica was terminated and climatic barriers intensified, although evidence of former connections is preserved in the Neogene plant fossil record and in the geographic affinities of the modern vegetation. Superimposed on these terrestrial and extra-terrestrial trends and processes was uplift of the Andes Mountain system. Highlands had been present along the western coast of South America since movement of that continent away from Africa began in the Cretaceous, but high mountains developed primarily in the Miocene, slightly earlier in the south (early Miocene) than in the north (early/middle Miocene).

By the beginning of the Miocene, virtually all plant fossils can be referred to modern families, many can be identified to genus, and, among leaf megafossils, a number can be recognized to species. Of the 12 modern plant formations discussed in Chapter 3, seven are evident in relatively modern form at the beginning of the Miocene—mangrove, beach/strand/dune, freshwater herbaceous bog/marsh/swamp, aquatic, lowland Neotropical rain forest, lower to upper montane broad-leaved forest, and coniferous forest (to the extent that stands of *Araucaria* and *Podocarpus* are placed in this formation rather than as associations in the broad-leaved forest). Greater seasonality in rainfall and temperature had reached a point at the beginning of the middle Miocene that pre-adapted elements were assembling into recognizable and expanding communities of shrubland/chaparral–woodland–savanna and grasslands. Later in the Miocene and especially in the Pliocene, the same became true for deserts, tundra, and alpine tundra.

Argentina and Chile (Figs. 7.66–7.71)

Plant microfossils are known from two early Miocene sections of the Monte León Formation along the coast of Santa Cruz Province of Argentina (Barreda & Palamarczuk, 2000c; Tables 7.2, 7.3), but the preservation is only fair and reworked Cretaceous palynomorphs are present from a tectonic reactivation event, requiring caution in attempting paleoenvironment and paleocommunity reconstructions. The megafossil *Casuarina patagonica*, a present-day Australian genus (Fig. 7.72), and pollen of the mimosoid legumes *Acaciapollenites myriosporites* and *Polyadopollenites* (= *Anadenanthera* aff. *macrocarpa*) were recovered from the early Miocene Chenque Formation of Chubut Province (Barreda & Caccavari, 1992; Palamarczuk





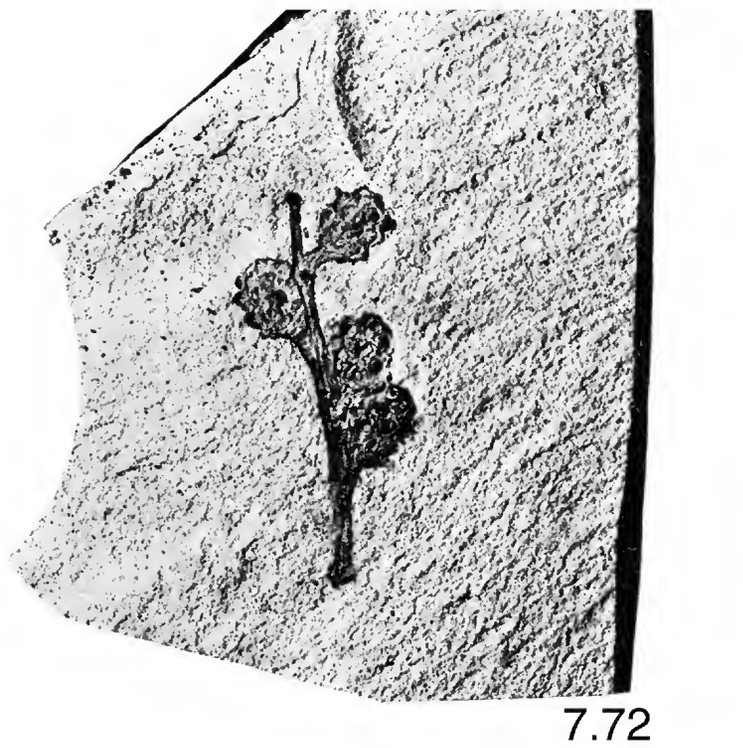


Figure 7.66. *Calliandra* sp. from the middle Miocene La Ollita Formation, San Juan Province, Argentina. Reprinted from Caccavari and Barreda (2000), with permission of Elsevier Science Publishers, Amsterdam.

Figures 7.67–7.71. Fossil pollen from the ~middle Miocene Yeso Series, San Juan Province, Argentina. 7.67. *Cyperaceaepollis neogenicus*. 7.68. *Striatricolporites gamerroi*. 7.69, 7.70. *Tubulifloridites antipodica* (Compositae, short-spine). 7.71. *Multisiapollis viteauensis* (Compositae, complex *Vernonia* type). From Barreda et al. (1998). Used with permission of the Asociación Paleontológica Argentina, Buenos Aires.

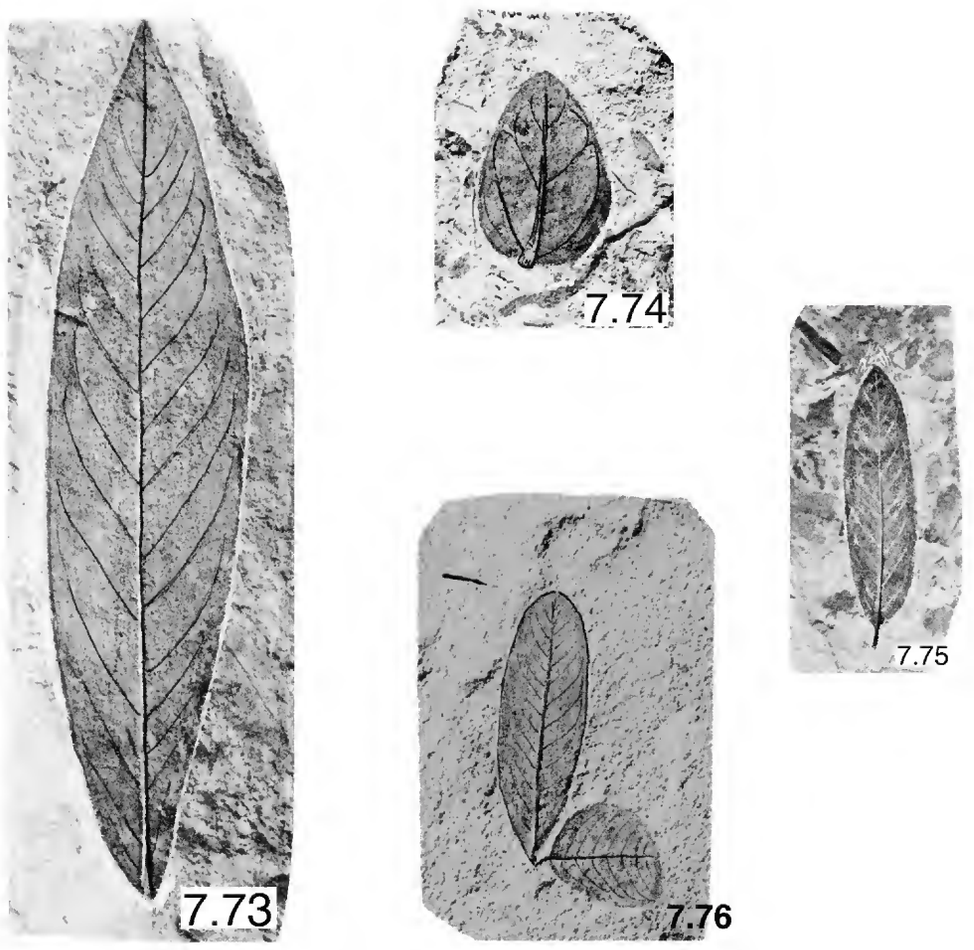
Figure 7.72. *Casuarina patagonica* from the Miocene of Chubut Province, Argentina. From Frenguelli (1943a). Used with permission of the Museo de La Plata, Universidad Nacional de La Plata, Argentina.

& Barreda, 1998; see also Table 7.1, early Miocene). The flora represents a warm and humid climate, and *Acacia* and *Anadenanthera* are mostly genera of warm habitats. *Acaciapollenites myriosporites* is known from the Tertiary of Australia, while *Anadenanthera* is a genus of two species in Brazil. Context information is available from a rich vertebrate fauna from the early Miocene Santa Cruz Formation of southeastern Patagonia (Tauber, 1997a, b; see also Barreda & Bellosi, 2003). Trends from the base to the top of the formation include a decrease in diversity, an increase in the number of species with euhypsodont teeth and a decrease in those with brachyodont teeth, glyptodontids and toxodontids become more diverse, megatheroideid average body size is reduced, and protheroteid diversity decreases. The vertebrate record is interpreted to reflect a climate that is becoming seasonally drier.

Late Miocene vegetation is represented by palynomorphs in several formations, including the Chiquimil (Mautino & Anzótegui, 1998, 2000), Palo Pintado (Anzótegui, 1998), Barranca Final (Guler et al., 2001), and Puerto Madryn (Palazzesi & Barreda, 2004). They record a drop in sea level, consistent with extensive glaciations on Antarctica and the expansion of glaciation in the Arctic. Pollen of the Poaceae, Amaranthaceae–Chenopodiaceae, Asteraceae, and *Ephedra* suggest seasonally dry conditions along the coast with *Ephedra* likely growing in the edaphically drier coastal sands.

Climates in northwestern Argentina adjacent to the rising Andes Mountains toward the end of the Neogene can be reconstructed using paleosol and stable isotope evidence. The mountains eventually reached an elevation of 5500 m, and the effect on the environments of the eastern slopes is preserved in the Santa María Basin (27°–26°S, 1600–2000 m; Kleinert & Strecker, 2001). Marine regression ended after 12 Ma, and

a dendritic riverine environment with seasonally dry climates developed. Waterlogged soils are evident between 9 and 7 Ma, after which time the area was drained by the rise of the Sierra Aconquija and the Cumbres Calchaquíes. In the Lauca Basin of northern Chile, sedimentary succession shows a trend toward increasing desiccation between 6.4 and 3.7 Ma (Gaupp et al., 1999). In the Santa María Basin, carbon isotopes indicate that trees and shrubs were prominent. Then between 5 and 3 Ma, herbs and grasses increase, followed by aridification at 2.5 Ma (late Pliocene) when the western mountains began casting a rain shadow to the east. This is also recorded by the dry caviomorph rodent fauna in the late Pliocene San Andrés Formation in coastal east-central Argentina (Verzi & Quintana, 2005). By this time glaciers were forming on the highest peaks, and the dry Pampean plains (estepa arbustiva árida and semiárida; Chapter 3) were experiencing the climatic vicissitudes of the oncoming ice age.



Figures 7.73–7.76. Plant fossils from the Pliocene of the Department of La Paz, Bolivia. 7.73. *Cassia ligustrina*. 7.74. *Cuphea antiqua*. 7.75. *Gaylussacia tertiaria*. 7.76. *Platypodium potosianum*. From Berry (1939b).

Uruguay, Paraguay, Bolivia

There are no Neogene floras published for Uruguay or Paraguay, and in Bolivia most studies were made in the early 20th century or earlier (Engelhardt, 1887; Britton, 1892; Berry 1917, 1939b, 1940; Singewald & Berry, 1922). More recent paleobotanical information has been incorporated into geologically based estimates on the uplift history of the Central Andes (Gregory-Wodzicki et al., 1998; Gregory-Wodzicki, 2000; Graham et al., 2001). Two methods can be used for this purpose. One is to determine the MAT from coeval floras deposited near sea level and at higher elevations, then use an approximate global average lapse rate (e.g., 5.5° C/km) to calculate the upper paleoelevation (Chapter 1, Topography; I: pp. 207–210; Molnar & England, 1990). The other is to reconstruct the plant formations represented in a fossil flora located at a high elevation, determine the elevational ranges of comparable extant communities, and estimate the amount of uplift necessary to have raised the fossil flora to its present position. Both approaches have limitations, including the availability of suitable floras, and the results must be compared with information from geomorphology (patterns of stream incision; thickness of eroded sediments in adjacent basins) and enthalpy calculations (Forest et al., 1995, 1998). In the Central Andes of Bolivia paleobotanical and paleopalynological studies based on the modern analog method have provided estimates of uplift that are generally consistent with independent lines of inquiry.

Four plant megafossil assemblages are known from the Altiplano of Bolivia and have been used to reconstruct paleoclimates and Andean uplift history—the late Oligocene–early Miocene Chucal flora, the early-middle Miocene Corocoro–Potosí flora (Figs. 7.73–7.76; radiometrically dated at between 13.8 and 20.7 Ma [middle Miocene; Gregory-Wodzicki et al., 1998]), the middle Miocene Jakokkota flora, and the Pislepampa flora (Figs. 7.77, 7.78). The latter is located ~20 km northeast of Cochabamba in the Puna at 3000 m where the present vegetation is a grassy páramo of *Stipa ichu*. The megafossils were studied by Berry (1922b) and considered to be Pliocene in age. Plant microfossils from the same site include the Vernonieae type of Asteraceae pollen that appears in the Mio–Pliocene; thus, the age of the Pislepampa flora is estimated at ~6–7 Ma.

The composition of the Pislepampa flora is given in Table 7.2, and numerical representations and the elevational ranges of similar living species are shown in Table 7.4. The paleocommunity most relevant to estimates of the paleoelevation of the Altiplano at 6–7 Ma is the cloud forest (bosque montano húmedo; Fig. 3.139). Pollen of *Podocarpus* (*Prumnopitys*) and cf. *Oreopanax* was present (Figs. 7.79, 7.80), and they occur together in the modern cloud forest (Fig. 7.81). Today this plant formation grows between 1200 and 3200 m elevation. The presence of palms and possibly *Cavanillesia* suggests deposition near the lower limit of this range, and the fossil leaves are large and all have entire margins, indicative of moist lowland tropical vegetation (I: pp. 124–128). Thus, it is likely that the fossil flora grew at the lower limits of the cloud forest where elements of the bosque Amazónico extended upland along the eastern slopes of the proto-Andes. This suggests a paleoelevation of ~1400 m (<1500 m fide Berry, 1922b, based on megafossils). The paleobotanical evidence indicates the flora was elevated from 1400 m to its present site at 3600 m during the past 6–7 Ma. When other factors are taken into account (climatic change, local uplift; Graham et al., 2001, pp. 1554–1555), it is estimated that from one-third to one-half of the present elevation of the Altiplano was attained during the past 10 Ma or less. Recall from Chapter 2 that recent geological evidence suggests the Altiplano was uplifted ~3700 m to its present maximum heights between 10.3 and 6.7 Ma.

Estimates of climate in the Eastern Cordillera during the

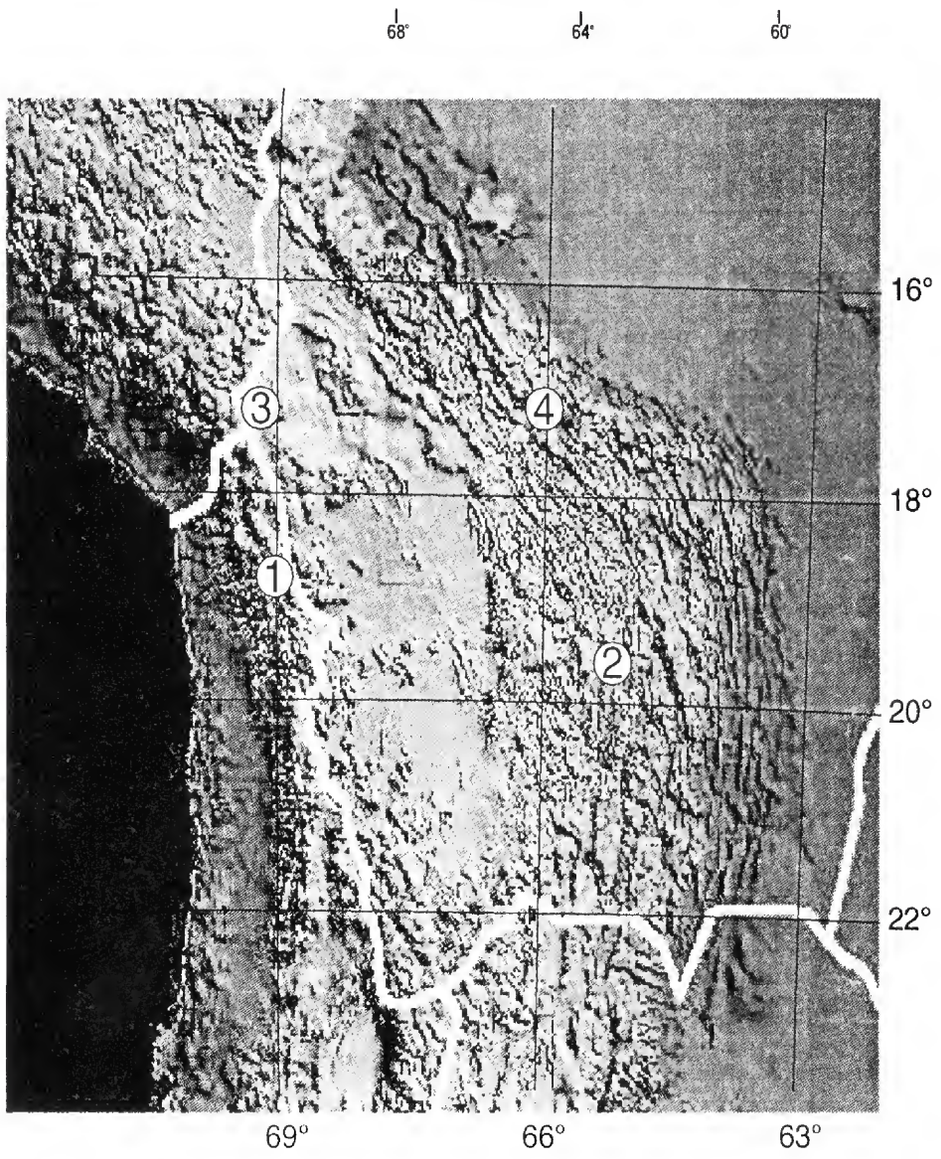


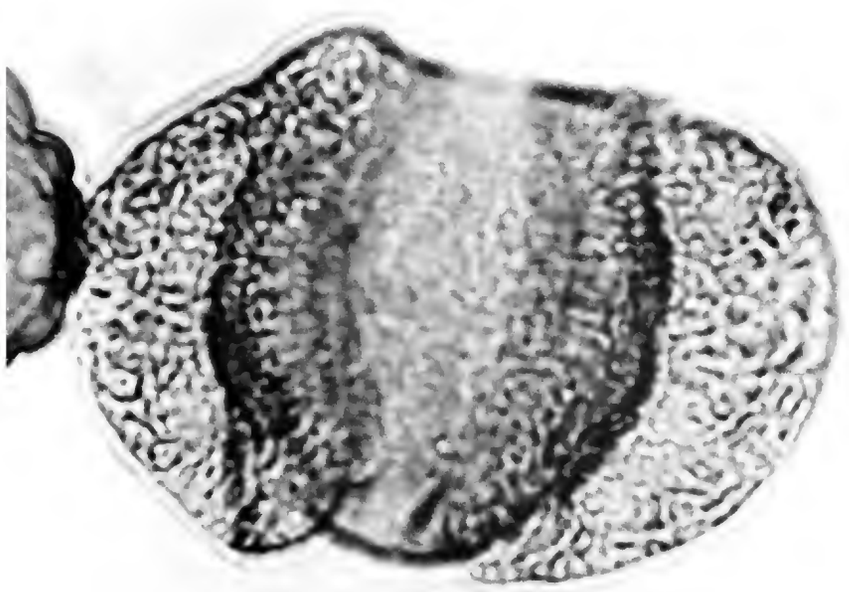
Figure 7.77. Relief map of the Central Andes (U.S. Geological Survey 30 arc-second digital elevation model) as processed by the Cornell Andes Project showing the location of four Neogene floras: 1. Chucal, 2. Potosí, 3. Jakokkota, 4. Pislepampa. From Graham et al. (2001), used with permission of the Botanical Society of America, St. Louis.

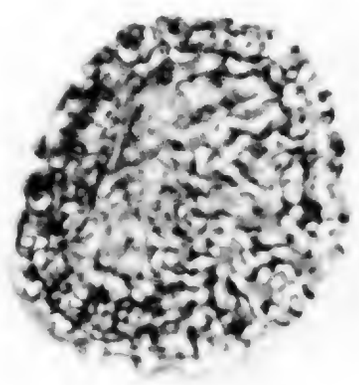
Mio–Pliocene can be made from temperature and rainfall within the present-day cloud forest. These values range between 10° and 20° C and 1000 to 3500 mm. Assuming that the Pislepampa fossil flora represented the lower range of the community, MAT would have been ~20° C and MAP between ~1000 and 1500 mm. Presently, annual rainfall at La Paz (3600 m) is 270 mm, and at Cochabamba (2534) it is 230 mm.

Among the paleocommunities suggested by the Neogene megafossil and microfossil floras are the lowland Neotropical rain forest and the lower to middle montane broad-leaved forest. In the relatively low elevations of the Central Andes, the present dry to arid vegetation (shrubland/chaparral–woodland–savanna) to the west of the mountains and in the interandean valleys was just developing in the Mio–Pliocene and was not extensive, consistent with global paleobotanical and climatic trends. The high-altitude páramo, and especially a grassy páramo, was not yet present as evident from the geological evidence and the meager representation of grasses in both the megafossil and microfossil record.

There is some context information by which other aspects of the vegetation can be inferred. MacFadden et al. (1994) analyzed the ^{13}C in tooth enamel from South American mammals in fossil deposits spanning the interval from 25 Ma to 7500 years B.P., including samples from the Bolivian Andes at elevations between 3200 and 4000 m. Carbon isotope values lowered from between 10.7% and 7.5% in the early and middle Miocene to 8.2%–5.5% in the late Miocene. This suggests a shift in prominent food reserves from C_3 shrubs and nongrassy herbs to C_4 grasses. In the Plio–Pleistocene, at high-elevation sites (>3000 m), enamel isotopes reflect grasses, while at middle to lower elevations the vegetation was a mixture of

Figure 7.78. The plant fossil locality at Pislepampa with field assistant Luis Huanca. From Graham et al. (2001), used with permission of the Botanical Society of America, St. Louis.





Figures 7.79 (above), 7.80 (right). Fossil pollen from the Mio–Pliocene Pislepampa flora, Bolivia. 7.79. *Podocarpus* (*Prumnopitys*). 7.80. cf. *Oreopanax*. From Graham et al. (2001), used with permission of the Botanical Society of America, St. Louis.

C_4 and C_3 plants. MacFadden et al. (1994) interpret the fossil mammal and carbon isotope evidence to mean that "the present-day biotic communities of the Central Andes were established during the late Miocene and early Pliocene prior to about 3.5 Ma." This is consistent with the paleobotanical evidence for the origin and history of the páramo as generally understood.

Peru

Berry (1919) provides line drawings of 14 species from an unnamed formation in northern Peru (Table 7.3), and although he notes that the collection "leaves much to be desired from the point of view of the correct botanical determination of the species…," there are several aspects of the flora that are instructive. One is that the locality is rather precisely located about 20 miles south of Tumbes and 200–300 feet inland from the shore of the Pacific Ocean. If it still exists, the site could be re-collected for plant megafossils. Also, the fossils are preserved in a clay lens overlying a bed of lignite that seems ideal for the preservation of plant microfossils. The present vegetation is coastal *Rhizophora* mangrove with semi-desert *Sesuvium* and dry woodland with *Prosopis* along the river valleys of the eastern slopes of the Andes Mountains. Even though identifications of the leaf fossils are tentative, the illustrations show that several are large and entire margined, suggesting that conditions were more humid than at present. However, the fragmentary condition of the fossils indicates transport, possibly from some distance up the river valley, into the lagoonal muds where the leaves are preserved. If the beds are Burdigalian (early Miocene) in age as favored by Berry (1919), deposition occurred when the drying effect of the cold Humboldt Current was just being augmented by substantial heights in the Andes Mountains. Paleoenvironmental interpretations would be aided considerably with study of the plant microfossils, assuming biological affinities were established, by providing a more complete inventory of the past regional vegetation. The Miocene Pebas Formation (18–10 Ma) extends into northeastern Peru (Solimões Formation, see Brazil, this chapter) and contains amber with diverse insect, arachnid, and microfossil inclusions of cyanobacteria (Nostocaceae), eubacteria, fungal spores, algae (*Scenedesmus*), lichen fragments, and a single pollen (Proteaceae; Antoine et al., 2006).

A Peruvian object of interest is one described by Knowlton (1919) as a fossil ear of corn (*Zea antiqua*; Fig. 7.82), "hardly likely to be younger than at least several thousand years," and subsequently cited in papers discussing the origin of maize (e.g., Collins, 1919, 1923). According to Brown (1934), it was obtained by W. F. Parks of St. Louis, Missouri, from a curio

Figure 7.81. Cloud forest vegetation near Comarapa, Bolivia. Note the presence of *Podocarpus* (*Prumnopitys*; tree projecting above the low canopy to the right) and *Oreopanax* (palmate-leaved plant in the center of the photograph). From Graham et al. (2001), used with permission of the Botanical Society of America, St. Louis.

Table 7.3. Age of Cretaceous and Tertiary formations/floras of South America cited in the text and Tables 7.1 and 7.2 according to the original authors, and radiometric dates (RD). Numbers in parentheses for Cretaceous and Paleogene formations/floras refer to references in Table 7.1; those for Neogene formations/floras refer to references in Table 7.2.

Formation/flora	Time	Age (Ma)
	Cretaceous, Paleogene	
Argentina		
Springhill (1, 2)	Berriasian–Valanginian	132–121
Various sites (3)	late Berriasian–Valanginian	
La Amarga (7)	Barremian	127–121
Baqueró (4, 5)	Aptian	121–112
Gorro Frigio (6)	Aptian	
Mata Amarilla (99, 11)	Albian (Coniacian, see Romero, 1986)	112–99
San Jorge/Magallanes (8) basins (3 floras)	Aptian–Turonian, Coniacian, Maastrichtian	71.3–65
Cañadón Seco (10)	Albian–Cenomanian to early Turonian	
Allen (18)	late Campanian to Maastrichtian	71
Jagüel (18)	Maastrichtian–Danian (K/T boundary)	71–65
La Colonia (21)	Maastrichtian	
Ciénaga del Río Huaco	Maastrichtian (Limarino et al., 2000)	
Paso del Sapo (17)	Late Cretaceous	
Malargüe (20)	Late Cretaceous	
Río Blanco (12)	Late Maastrichtian/Danian	~66–61
Bororó (12, 24, 29, 30)	Danian	65–61
Cerro Dorotea (12, 13, 15, 16)	Danian	65–61
Salamanca (12, 22, 29, 30)	Danian	
Pedro Luro (19, 36)	Danian	
Maíz Gordo (33)	Paleocene	65–54.8
Mealla (Salta Group; 37)	middle to late Paleocene	
Río Chico (12, 28)	Thanetian	57.9–54.8 Ma
Laguna del Hunco (25, 26, 27)	Thanetian	RD-57 ± 3 Ma (Archangelsky, 1974); ~52 Ma (Wilf et al., 2003)
Tunal (31, 32)	Paleocene	
Lumbrera (34, 35)	late Paleocene to early Eocene	
Río Pichilefú (Ventana Formation; 41)	early Eocene (see Romero, 1986, originally early Miocene)	54.8 Ma
Río Chenqueniyeu (1)	early Eocene (see Romero, 1986, originally Miocene)	
Ñirihuau (40)	Eocene	54.8–33.7
Río Turbio (15, 16, 38, 42, 43, 44, 45)	late middle Eocene to early late Eocene	~45
Sloggett (46)	late Eocene	37–33.7
Pachaco (50)	late Eocene to Miocene	
Río Guillermo (15)	early Oligocene	33.7–28.5
San Julián (51)	late Oligocene	28.5–23.8
Cullen (47)	Miocene (Zamaloa, 2000)	
Chenque (52)	early Miocene	
Chile		
Cerro Guido (53)	Maastrichtian	71.3–65
Quiriquina (55)	late Senonian (Maastrichtian)	
[Various southern Chile localities; 54]	late Cretaceous to Eocene (?)	
Curanilahue (56, 59, 64) (Lota, Coronel members; 58, 59)	Paleocene/early Eocene/Oligocene	
Quinamávida (57)	early Eocene	54.8–49.0
Tribueco	early Eocene	
El Arrayán	early/middle Eocene	
	Eocene/Eo–Oligocene	
Cerro Las Aguilas	Eo–Oligocene	
Colbún (57)	early Eocene	54.8–49
Leña Dura (60)	Eocene	54.8–33.7
Lonquimay (61)	Eocene/middle Oligocene (Miocene?)	
Guadal (62, 63)	Oligo–Miocene/Miocene	~26–7.1
Río Zeballos (62)	Oligo–Miocene/Miocene	
Bolivia		
Eslabón (65)	Maastrichtian	71.3–65
Flora (65)	Paleocene (?)	
Potoco (66)	late Eocene/early Oligocene	
Peru		
Vivian (67, 68)	Late Cretaceous (Campanian)	

Table 7.3. Age of Cretaceous and Tertiary formations/floras of South America. *(Continued)*

Formation/flora	Time	Age (Ma)
Pariñas Sandstone, Negritos (69, 70)	early Eocene	54.8–49.0
Restin/Chacras (71)	early Eocene	
Ecuador		
Ancon Sandstone (72)	Eocene	54.8–33.7
Colombia		
Région de Mesas et Questas (Pons, 1988)		
Rosablanca (73, 74)	Early Cretaceous (early Barremian)	~127
Paja (74)	late Barremian	~122
Région de Quetame Massif		
Lower Villavicencio (74)	Aptian	121–112
Middle Villavicencio (74)	early Aptian	
Late Villavicencio (74)	upper Albian to lower Cenomanian	
Gacheta (74)	Aptian	121–112
Une (78d)	late Aptian–early Cenomanian	
Guaduas (79)	Maastrichtian	71.3–65
Cimarrona (80)	Maastrichtian	
Colón, Molino (81)	Maastrichtian	
Guaduas (82)	Maastrichtian–Paleocene	
Hato Nuevo (83)	late Paleocene	57.9–54.8
Cerrejón (83)	late Paleocene	
Arcillas de El Limbo (85)	late Paleocene	
Lisama (85)	late Paleocene	
La Paz (85)	early to middle Eocene	54.8–41.3
Mirador (85, 86)	early to middle Eocene	
Los Cuervos (86)	early to middle Eocene	
San Fernando (85)	middle Eocene	
No formations (Berry, 1924b, c, 1924–25; Huertas G., 1977; 78a)	Eocene/Oligocene?	~34
No formations (Schuler & Doubinger, 1970; 87)	Eocene/Oligocene?	
Planeta Rica (78b)	late Oligocene/early Miocene	
Antioquia (78c)	late Oligocene/early Miocene	
Venezuela		
No formation (Berry, 1939a; 88)	Eocene	54.8–33.7
No formation (Sinanoglu, 1983; 90)	?Aptian–early Albian	
Misoa (91)	middle Eocene	
Jarillal (92)	late middle Eocene	
Potreritos, Las Flores	late Eocene	
Guyana, Suriname, French Guiana		
Takutu (93)	Late Jurassic/Early Cretaceous	~145
Mackenzie, Montgomery (94)	Late Cretaceous/Paleogene	~65
Brazil		
Codó (99)	Cretaceous, Aptian	121–112
Maria Farinha (97b)	Paleocene	65–54.8
Itaquaquecetuba (98)	probably late Eocene	37.0–33.7
Continental Platform (100)	Late Cretaceous–Paleogene	
Neogene (Miocene, Pliocene)		
Argentina		
Arroyo Puipucón, Neuquén (1)	Miocene	23.8–5.3 Ma
La Lipela, Neuquén (2)	Miocene	
El Mirador, Chubut (3)	Miocene	
Morro Revancha, Río Negro (4)	Miocene	
Río Chalia, Santa Cruz (5)	Miocene	
Monte León (8)	early Miocene	23.8–16.4
Chenque (9)	early Miocene (see Table 7.1)	
Yeso Series (10)	Miocene, probably middle Miocene	
La Ollita (11)	middle Miocene	
Chiquimil (12)	late Miocene	
Barranca Final (13)	late Miocene	
Palo Pintado	late Miocene	
Puerto Madryn	late Miocene	

Table 7.3. Age of Cretaceous and Tertiary formations/floras of South America. *(Continued)*

Formation/flora	Time	Age (Ma)
Chile		
El Arrayán (14)	Oligo–Miocene	28.5–20.5
Río Calchaquí, Salta (6)	late Miocene	11.2–5.3
Filaret (15)	late Miocene	11.2–5.3
Navidad (16, 17, 18)	Miocene	
Coronel–Lota (19a)	Late Tertiary	
Bolivia		
Cerro Potosí (20, 21, 22)	Late Tertiary	
Corocoro, Potisí (23, 24, 25)	Pliocene	5.3–1.8
Agua Salada (26)	Pliocene	
Pislepampa (27)	Mio–Pliocene	
Peru		
Tumbes (28a)	Miocene (Burdigalian)	
Ecuador		
Punta Gorda (29)	Mio–Pliocene	
Loja (30)	Mio–Pliocene	
Loja, Tablayacu (31)	Mio–Pliocene	
Colombia		
Santa Ana (Río Magdalena), Cáucathales (32)	Mio–Pliocene	
Magdalena Valley (33)	Miocene	
Río Casanare (34)	Mio–Pliocene	
Río Cauca/Antioquia (35)	late Oligocene	
Mesa (36)	Late Tertiary	
Honda Group (37)	Miocene	
Corozal (38)	Late Tertiary	
Eastern Cordillera (39)	Pliocene	
Venezuela		
Betijoque (40)	middle to late Miocene	
Damsite Series (41)	late Miocene	
Chiquero (42)	Pliocene	
Maracaibo, Falcón, Eastern basins (43)	Oligocene–mostly Miocene–Pleistocene	
Trinidad		
Trinidad, Forest Sand et al. (44)	Miocene	
Pitch Lake (45)	Miocene	
Brazil		
Aramarý (46)	Pliocene	
Mocambo, Fonseca (47)	Pliocene	
Fonseca (48)	Pliocene	
Fonseca (49)	Pliocene	
Solimões Basin (50)	early–late Miocene	

shop in Cuzco, Peru. It turned out to be made of baked clay, still bearing marks of the tool used to fashion a small internal cavity into which oval pellets were sealed that rattled when the object was shaken. Thus, it seems destined together with the Early Cretaceous banana from Colombia to join the ranks of the unlikely.

Ecuador

Fossils of more certain identification, but equally intriguing, are fruits of *Juglans linki* from the Mio–Pliocene Punta Gorda Formation west of the Río Esmeraldas in Esmeraldas Province, northwestern Ecuador (Brown, 1946; Figs. 7.83, 7.84). If the age is correct, this would be the earliest convincing record of a northern temperate element in South America. The oc-

Figure 7.82. Supposed fossil ear of corn from Cuzco, Peru. From Brown (1934). Used with permission of the Washington Academy of Sciences, Washington, D.C.

Figures 7.83, 7.84. Fossil fruits of *Juglans linki* from the Punta Gorda Formation, Esmeraldas Province, Ecuador. From Brown (1946). Reprinted by permission of the *American Journal of Science*.

currence is of particular interest because it represents a genus with limited means of long-distance dispersal, and was present prior to the completion of the isthmian land bridge. Even at the time of near-closure, the landscape was low lying and supported tropical vegetation. For the moment, this apparently valid record of *Juglans* in presumably Mio–Pliocene deposits of Ecuador is an anomaly.

Megafossil floras from two Mio–Pliocene sites, Loja and Tablayacu, were described by Engelhardt (1895; Table 7.2), and the one from the dry interandean basin near Loja in southern Ecuador was restudied by Berry (1945a; Fig. 7.85). Burnham and Carranco (2004) have described *Loxopterygium laplayense* (Anacardiaceae) from the Cuenca and Loja basins. These specimens are similar to extant species in the seasonally dry forest of Argentina, Bolivia, Ecuador, and Peru. A legume, *Tipuana ecuatoriana*, is also known from the Miocene of Cuenca Basin in Ecuador (Burnham, 1995). The Humboldt Current had been exerting a drying effect along the coast since the opening of the Drake Passage (~34 Ma) and the beginning of extensive continental glaciation on Antarctica near the end of the Oligocene (~30 Ma). To the extent that the paleoelevation data from Bolivia apply to this section of Ecuador, the Andes Mountains were still about one-half of their present average elevation and did not fully augment the drying of the Humboldt Current by creating a rain shadow as at present. The elevation around Loja is ~3000 m and the Andes Mountains to the east are ~4500 m. The expectation is that the current differentiation into dry vegetation along the coast and in the interandean valleys, and moist vegetation on the upper and eastern slopes, would not have been as pronounced in the Mio–Pliocene. The Loja fossil flora has some elements collectively suggesting dry conditions, such as *Alchornea*, *Bauhinia*, *Bignonia*, *Bombax*, *Caesalpinia*, *Capparis*, *Cassia*, *Inga*, *Lonchocarpus*, *Pisonia*, *Rhamnidium*, *Serjania*, and *Tapiria*. It also includes more moist and tropical elements such as *Zamia*, *Couratari*, *Macrolobium*, *Myrcia*, *Myrciaria*, *Myristica*, *Nectandra*, *Persea*, *Phorodendron*, *Styrax*, *Tetracera*, *Trichila*, and *Vochysia*. The megafossils are not particularly fragmentary, and some larger specimens are intact, so the flora probably grew in the immediate vicinity. The sediments have not been examined for plant microfossils that would give a more regional picture of the plant formations, but it is likely that cloud forest and ceja species were present in the highlands. Thus, the history of the vegetation in this part of Ecuador closely reflects the rise of the Andes Mountains. Continuing increase in elevation would produce habitats suitable for páramo in Mio–Pliocene and later times.

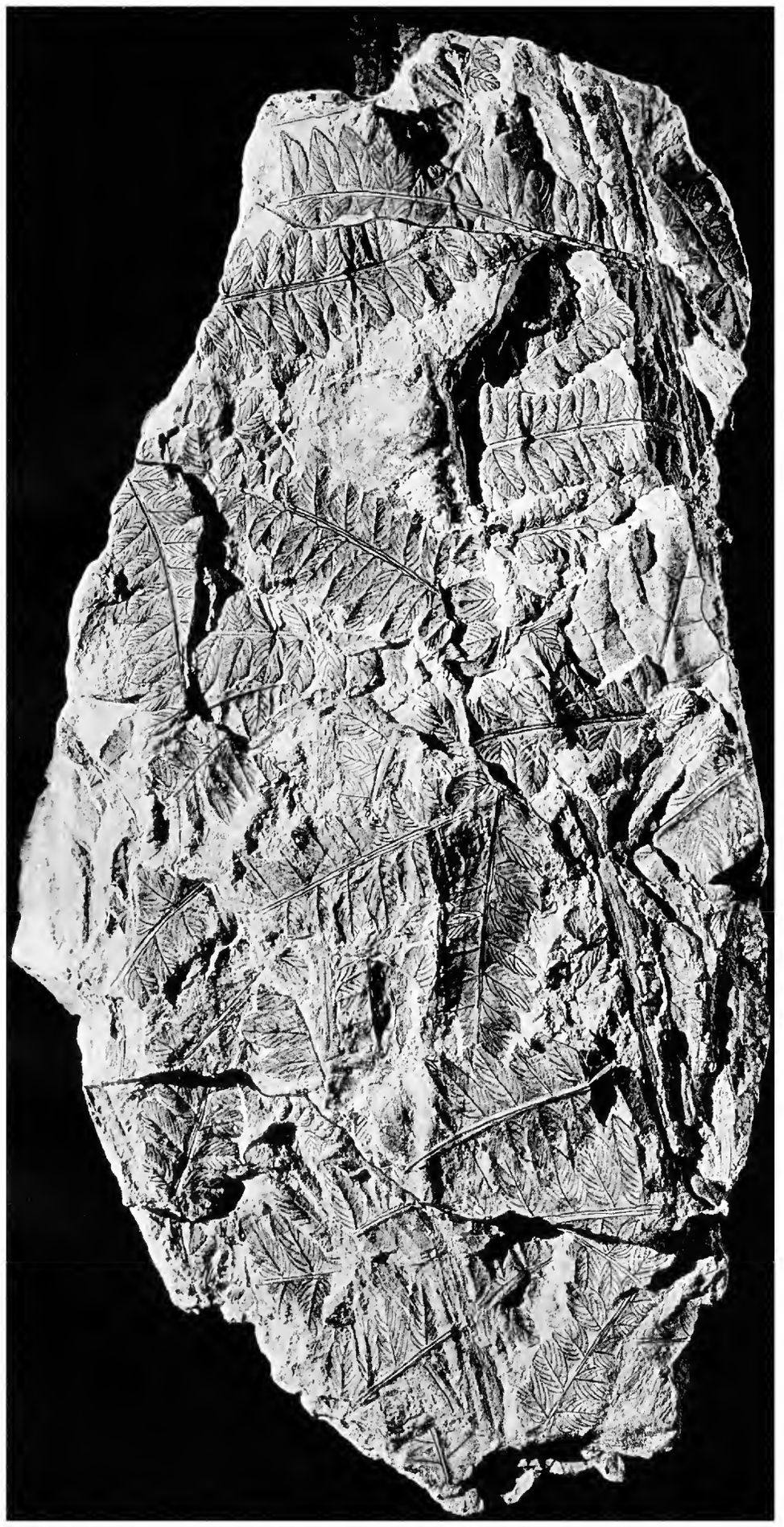


Figure 7.85. *Goniopteris cochabambensis* from the Mio–Pliocene of the Loja Basin, Ecuador. From Berry (1945a).

Colombia

Three megafossil floras of Neogene age from Colombia are described in the early literature (Engelhardt, 1895; Berry, 1936b, 1945b; Tables 7.2, 7.3), but the age is uncertain (Late Tertiary), many of the specimens are fragmentary, and all are illustrated by line drawings. The composition and leaf sizes suggest lowland tropical forest. One identification, illustrated

by a stylized sketch, is of the mangrove *Avicennia* from a locality along the Río Magdalena 350 miles inland from the present coast (Berry, 1936b). The area now is only a few hundred feet above sea level, and if the identification were confirmed and the age better established, it would help document when and how far inland the sea extended along the Magdalena estuary. It would also contribute to a more detailed reconstruction of Andean uplift history. A diverse mangrove vegetation is known to have been extensive and frequently present in northwestern Amazonia in the Neogene based on microfossil evidence (see later discussion).

In contrast to the meager information available on the Miocene vegetation in the early literature, a relatively good database has recently been generated for Pliocene vegetation (Fig. 7.86) from the Cordillera Oriental and vicinity and for Miocene faunas from the central Magdalena Valley. The faunas are from the Honda Group of middle Miocene age at La Venta (Kay & Madden, 1997). The site presently is at an elevation of <500 m and the MAP is ~1000 mm. A number of conclusions based on the composition and body sizes of the fauna are relevant for vegetational history, including an estimated rainfall of 1500–2000 mm/yr that today marks the transition between savanna and forest in the lowlands; a primarily forested habitat consisting of a riparian mosaic of shifting meandering rivers; and an extensive lowland Neotropical rain forest just to the east that pre-dated the principal uplift of the moisture-deflecting Eastern Cordillera in middle to late Miocene and Pliocene times.

Regarding the Pliocene vegetation, in addition to the atlas of Neogene plant fossils compiled by Wijninga (1996a), there are studies on the plant communities (Doubinger, 1976; Hooghiemstra, 1993, 1994a, b, 1995; Hooghiemstra et al., 1994; van der Hammen, 1995; Wijninga, 1995, 1996b, c, d; Wijninga & Kuhry, 1990, 1993), geochronology (Andriessen et al., 1993), and stratigraphy (Solé de Porta, 1960, 1961, 1963). These show that it was in the Pliocene, and especially in the Plio–Pleistocene transition, that the extant plant formations of Colombia, from the rain forest to páramo, were established. This is evident from the list provided by Wijninga (1996a; Table 7.2; Figs. 7.87–7.93) from which the following paleocommunities can be recognized (taxa are placed according to their principal occurrences, and several range into other habitats):

Shrubland/chaparral–woodland–savanna—*Connarus*, *Coussapoa*, *Ecclinusa*, *Humiriastrum*, *Psychotria*, *Rheedia*, *Sacoglottis*, *Xyris*, *Zanthoxylum*

Mangrove—*Zonocostites ramonae* (*Rhizophora*) present in the Maracaibo Basin and vicinity since the middle Eocene (Germeraad et al., 1968); *Avicennia* (?) in the Neogene of the Río Magdalena area (Berry, 1936b)

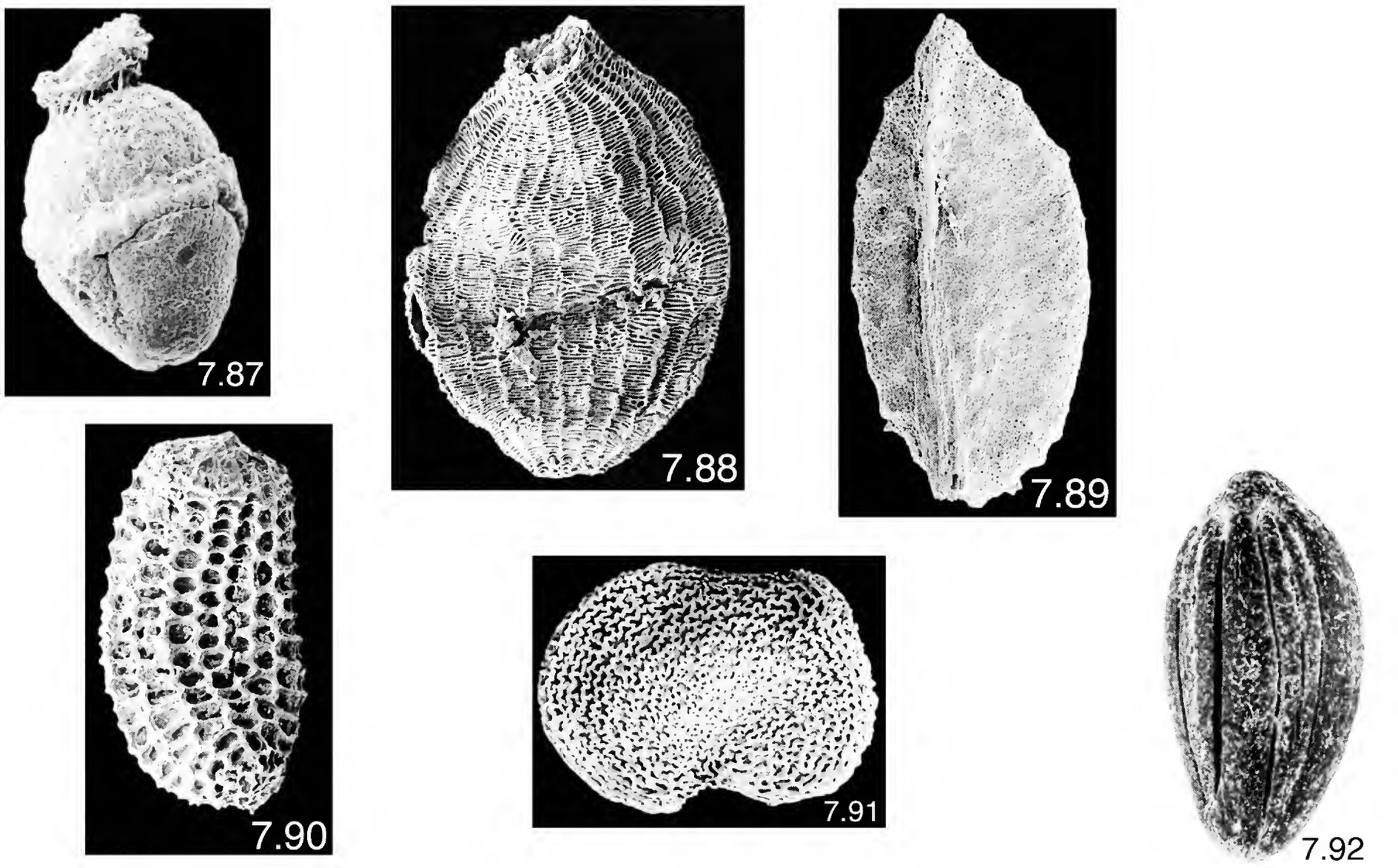
Freshwater herbaceous bog/marsh/swamp—*Sphagnum*, *Callitriche*, *Crassoretitriletes vanraadshoovenii* (*Lygodium*); trees of the rain forest/lower part of the montane broad-leaved forest extending into the swamps: *Amanoa*, *Ilex* (widespread), *Ludwigia*, *Machaerium* (climbing shrub or liana), *Macoubea*, *Macrolobium*, *Mauritia* (palm swamps), *Rheedia*

Figure 7.86. *Cyathea colombiensis* from the Late Tertiary Mesa Formation, state of Tolima, Colombia. From Pons (1975). Used with permission of Renate Remy and Denise Pons.

Aquatic—cf. *Spirogyra*, *Azolla*, Alismataceae, *Callitriche*, *Elatine* (to 3000–4000 m), Nymphaeaceae

Lowland Neotropical rain forest—*Selaginella* (widespread), *Danaea* (sea level to 2300 m), *Amanoa*, *Anacardium* (to 1800 m), *Anthurium*, *Astrocaryum*, *Brownea*, *Catopsis*, *Coussapoa* (some species to montane forest), *Cyclanthus*, *Ecclinusa* (most species below 200 m in non-flooded parts of the lowland rain forest), *Evodianthus*, *Hippocratea–Pristimera* (to ~1800 m), *Humiriastrum* (below 1200 m), *Iriartea*, *Macoubea*, *Mauritia*, *Parinari* (generally below 800 m), *Pouteria*, *Psychotria* (widespread), *Rheedia*, *Sacoglottis* (generally below 1200 m), *Symplocos* (some species to humid montane forest), *Vantanea* (below 800 m), *Virola*

Lower to upper montane broad-leaved forest—lower: *Cyclanthus* (below 1300 m); upper: *Decussocarpus* (in the Cordillera Oriental between 1800 and 2150 m with *Clusia*, *Ficus*, *Heliocarpus*, *Hieronyma*, *Quararibea*), *Podocarpus*, *Alchornea*, *Anthurium* (cloud forest above ~2700 m; elsewhere in Colombia 1750–3750 m), *Clethra*, *Ecclinusa* (mostly rain forest but a few species to 1300 m in wet montane and elfin forest with *Podocarpus*, *Clusia*, and *Stenopadus*), *Freziera* (commonly in cloud forest), *Gunnera* (damp habitats to subandean forest and páramo), *Hedyosmum*, *Ilex*, *Myrsine*, *Symplocos* (lower to rain forest), *Turpinia* (in Colombia uplands below 2500 m), *Vallea*, *Viburnum*, *Weinmannia*



Figures 7.87–7.92. Plant fossils from the Neogene of the High Plain of Bogotá, Colombia. 7.87. *Azolla* megaspore with attached massulae. 7.88. cf. *Juncus* seed. 7.89. *Cecropia* seed. 7.90. *Elatine* seed. 7.91. Solanaceae seed. 7.92. *Vantanea* seed. From Wijninga (1996a). Used with permission of the University of Amsterdam, Amsterdam.

Páramo—*Eleocharis*, *Gunnera*, *Xyris* (widespread), *Juncus* (widespread), *Ranunculus* (widespread but common in wet places in the high Colombian Andes), *Rubus* (dwarf species in páramo), *Scirpus* (widespread).

In addition to the taxa and the principal communities present, there is additional information on their time of appearance and the paleoelevation. Recall that the principal period of uplift of the Andes Mountains began somewhat earlier in the south (~Miocene to middle Miocene, ~23–14 Ma) than in the Central and Northern Andes (~middle Miocene to Mio–Pliocene, around 10–6 Ma). The study sites in the High Plain of Bogotá of the Cordillera Oriental are presently at altitudes between 2450 and 2820 m (Wijninga, 1995, 1996a). Sediments of the Tequendama Member of the Lower Tilatá Formation were deposited in a depression on a river floodplain before principal uplift of the mountains (Fig. 7.94). This is evident from the fossil flora composed of floodplain elements of the lowland Neotropical forest listed above, with river-transported pollen of *Podocarpus* from the highlands in the vicinity. The

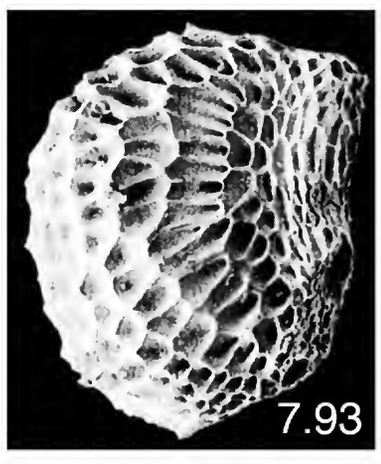


Figure 7.93. *Freziera* seed from the Pliocene of the Subachoque Valley (Cordillera Oriental, Colombia). Reprinted from Wijninga and Kuhry (1990), with permission of Elsevier Science Publishers, Amsterdam.

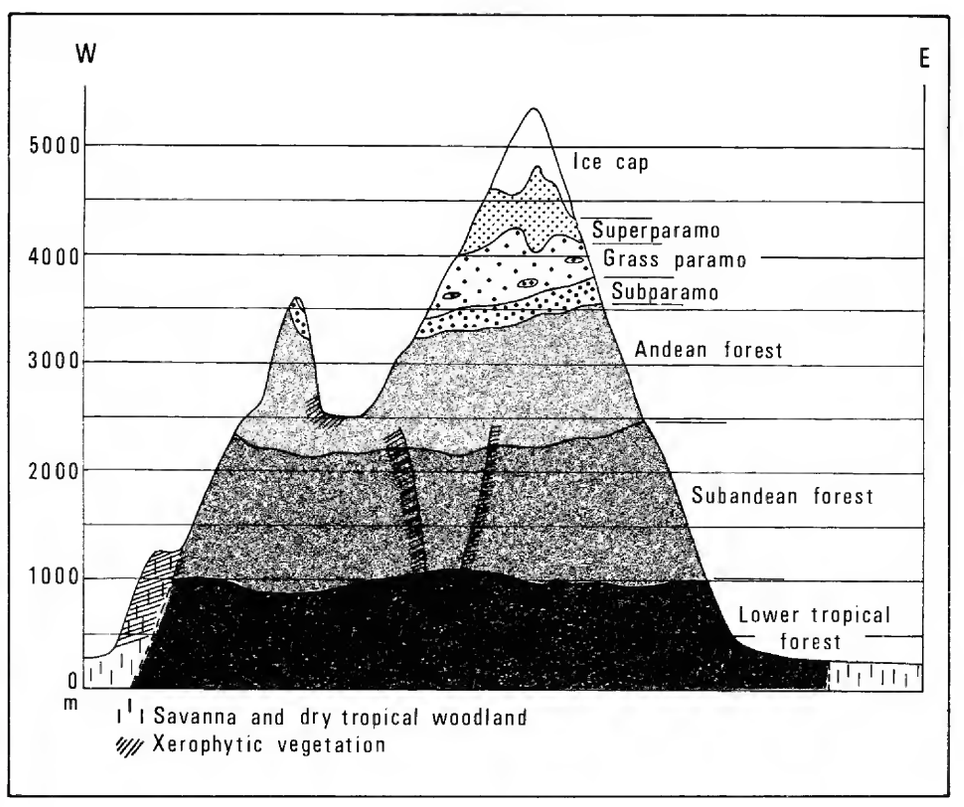


Figure 7.94. Present altitudinal zonation of vegetation in the Cordillera Oriental of Colombia. Reprinted from Wijninga and Kuhry (1990), with permission of Elsevier Science Publishers, Amsterdam.

age is middle(?) Miocene, and the estimated paleoelevation was 700 ± 500 m.

Fossils recovered from a peat section indicate a *Podocarpus* mire with numerous members of the lower to upper montane broad-leaved forest. Fission-trace zircon measurements give an age of 3.7 ± 0.5 Ma, and the approximate paleoelevation was 2000 ± 500 m. Fluvio-lacustrine sediments of the Guasca Member of the Upper Tilatá Formation preserve a vegetation near the upper limit of the present-day subandean zone. The age is late Pliocene (4–3 Ma). The elevation was 2200 ± 500 m and approaching modern heights.

Venezuela

The older literature on the Neogene paleobotany of Venezuela includes several papers by Berry (1922c, 1936a, 1937e, 1939c; Tables 7.2, 7.3). They are out of date and the identifications are suspect, but they can be used for locating plant-bearing localities, the matrix may preserve microfossils and material suitable for radiometric dating, and study of the leaf physiognomy could provide an indication of the climate. The palynological evidence, like that for the Cretaceous and Paleogene of Venezuela, has been used primarily for geological purposes (e.g., stratigraphy, zonation, correlation, facies analyses; Lorente, 1986). As a result, there is limited information for reconstructing vegetation history. However, the sequence of appearance of several taxa in northern South America, particularly for the Maracaibo Basin and vicinity, is well documented. This is due in large part to efforts by Jan Muller and others to establish the biological affinities of the microfossils based on careful study and adequate reference collections (Muller in Germeraad et al., 1968). Using the stratigraphic information given in Germeraad et al. (1968) and Muller (1981, Muller et al., 1987; Table 7.3), the early occurrences in northern South America of several groups as listed in Lorente (1986) are given below. All extend to the Recent in the region unless otherwise indicated. A comparison with Fig. 7.1 shows that the identifications do not contradict developing phylogenies (family names fide original authors):

Nypa (*Spinozonocolpites*; Palmae)—Maastrichtian to middle late Eocene
Ilex (*Ilexpollenites*; Aquifoliaceae)—Maastrichtian (oldest record is in the Maastrichtian of California; later in the Paleocene of Argentina)
Annonaceae (*Proxaperites*)—Paleocene
Poaceae (*Monoporites*)—Paleocene
Mauritia (*Mauritidites*; Palmae)—Paleocene
Crudia type (*Striatricolpites*; Leguminosae)—late Paleocene
Crenea (*Verrutricolporites*; Lythraceae)—early Eocene
Cuphea (*Striasyncolpites*; Lythraceae)—middle/late Miocene
Pelliceria (*Psilatricolporites*; Pelliceriaceae)—early Eocene
Caesalpinia type (*Margocolporites*; Leguminosae)—early middle Eocene
Cyperaceae (*Cyperaceaepollis*)—middle Eocene
Alchornea (*Psilatricolporites*; Euphorbiaceae)—middle Eocene
Rhizophora (*Zonocostites*; Rhizophoraceae)—late middle Eocene
Catostemma (*Jandufouria*; Bombacaceae)—late Eocene
Symphonia (*Pachydermites*; Guttiferae)—late Oligocene
Compositae (long/short-spine, *Echitricolporites*)—Oligo–Miocene
Compositae (complex *Vernonia* type)—late Miocene
Chenopodiaceae–Amaranthaceae (*Psilaperiporites*)—early Miocene
Pachria (*Bombacacidites*; Bombacaceae)—early Miocene
Acanthaceae (ornate *Beloperone* et al. types; *Multiareolites*)—middle-late Miocene
Orchidaceae (*Orchideamasulites*)—Late Tertiary–Oligocene
(?)*Alnus* (*Alnipollenites*)—Pleistocene

Brazil

Our knowledge of the Neogene vegetation of Brazil is limited because much of the region is lowland tropics where conditions are not conducive to the preservation of megafossils, many investigations of plant microfossils have been stratigraphic in nature, and the information that does exist must be applied across a vast region. Also, studies of the most extensive megafossil floras were published near the turn of the last century and none have been revised. Berry (1936c, p. 568) noted, "It seems quite evident from the material that I have seen from Fonseca [Minas Gerais] that it is nothing more than a sample and that intensive collecting would disclose a large and well preserved flora." The sediments include clays, shales, and lignites that very probably contain plant microfossils.

Samples of early to late Miocene age have been obtained from the Solimões Basin of Brazil (Solimões Formation) and the Amazonas Basin of Colombia and Peru (Pebas Formation; Hoorn, 1993a, b, 1996; Figs. 7.95, 7.96). These are north of the Acre Basin studied by Berry (1937f; Duarte, 1970), and east of the Bogotá Basin that in the middle Miocene was at an elevation of ~700 m or less (Wijninga, 1995, 1996a). A catalog of fossil palynomorphs from the Miocene of northwestern Amazonia is given in Table 7.2 based on Hoorn (1994a; see also Hoorn, 1994b, c). Throughout the sections, there is no evidence for desert or shrubland/chaparral–woodland–savanna plant formations (*Acacia*, widespread; the polycolpate ephedroid-like grains are referred to *Spathiphyllum*). Grass pollen is associated with other taxa that suggest it came from floating meadows in an alluvial plain environment, rather than dry grasslands. An important indicator plant in the basin sediments is *Rhizophora* because it reflects lowland paleoelevations and marine inundations. The fact that mangroves fluctuate in abundance throughout the section indicates periodic marine incursions and regressions during the Miocene and a dynamic environment for the biotic communities. The principal plant formations present in the Solimões and Amazonas basins during the Miocene, based on the taxa given in Table 7.2, were:

Mangrove—*Acrostichum*, *Avicennia*, *Hibiscus* type, *Pelliceria*, *Rhizophora*. Times of abundant mangrove taxa

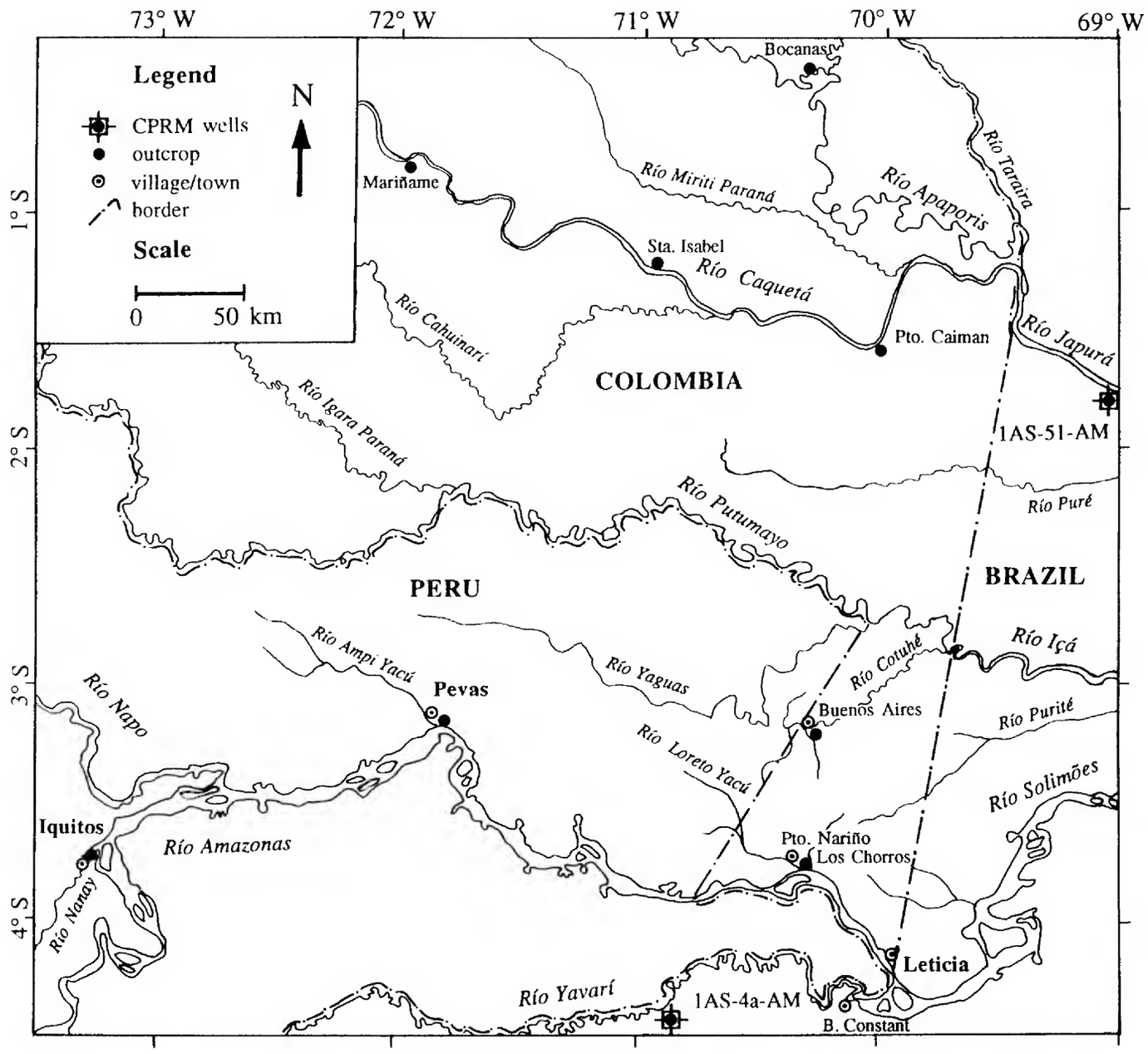


Figure 7.95. Map of well and outcrop locations, northwest Amazonia, Brazil, Colombia, and Peru. Reprinted from Hoorn (1993a), with permission of Elsevier Science Publishers, Amsterdam.

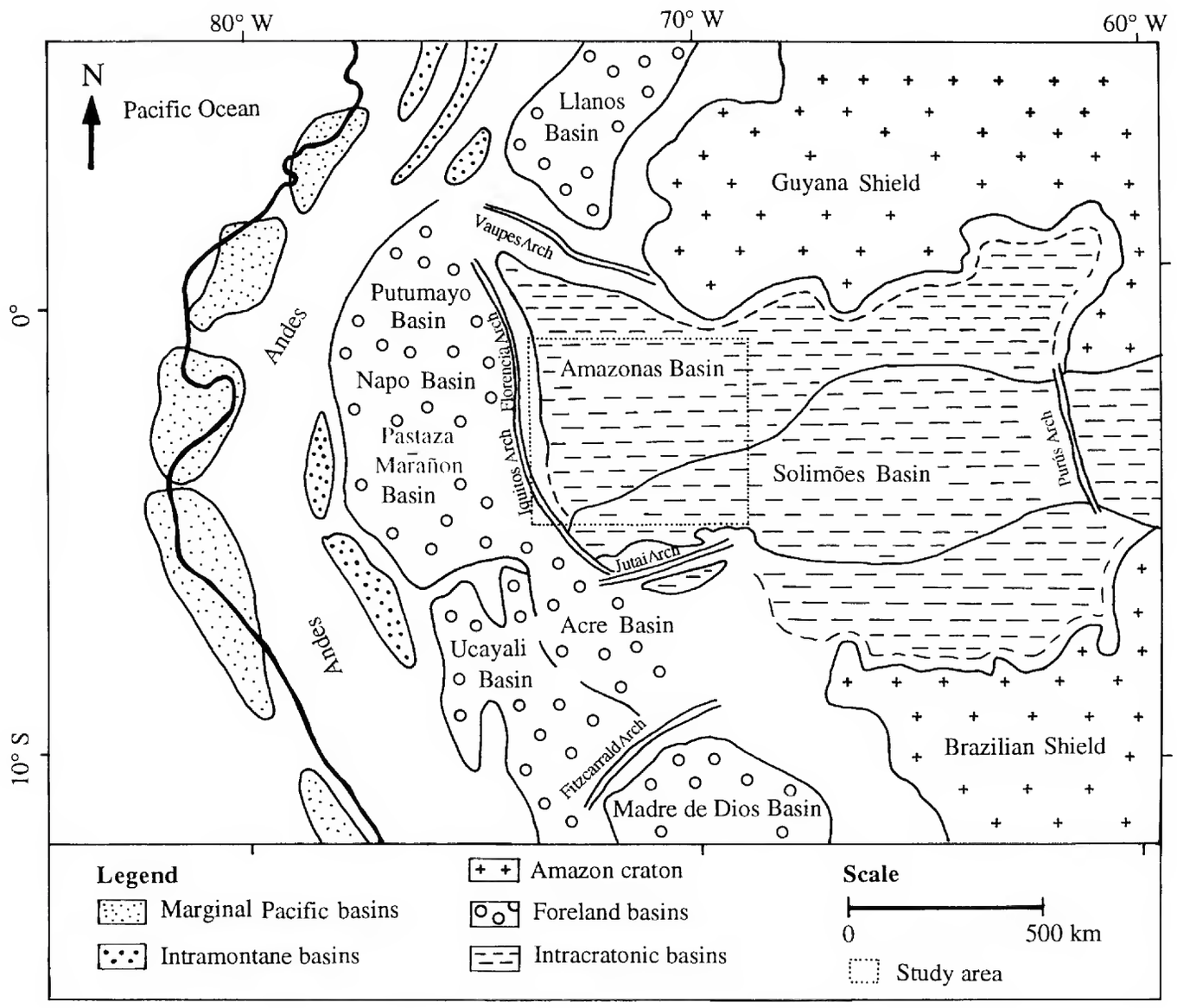


Figure 7.96. Sedimentary basins of northwest Amazonia, Brazil, Colombia, and Peru. Reprinted from Hoorn (1993a), with permission of Elsevier Science Publishers, Amsterdam.

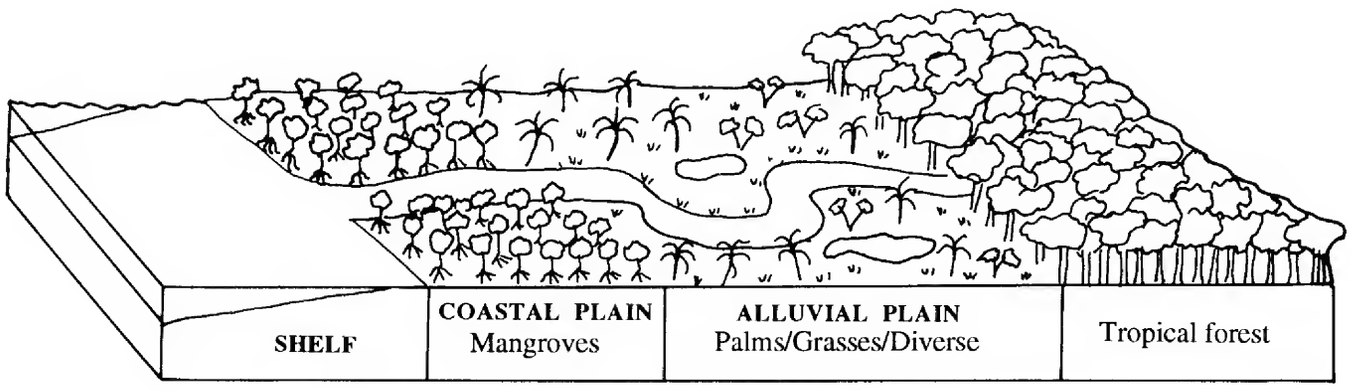


Figure 7.97. Reconstruction of Miocene communities of northwest Amazonia. Reprinted from Hoorn (1993a), with permission of Elsevier Science Publishers, Amsterdam.

correspond to high stands of global sea level in the Burdigalian, Langhian, and Serravallian. In the earliest Burdigalian, sediment composition indicates incursions came both from the east (Guayana Shield–type sediment) and from the west through low corridors in the early Andes Mountains.

Beach/strand/dune—The presence of this formation is inferred from the setting, sediment types (sand), and the presence of mangroves, even though pollen of prominent species of the community cannot be distinguished (e.g., members of the Poaceae, Asteraceae).

Freshwater herbaceous bog/marsh/swamp (with associated riparian, swamp forest)—*Alchornea* (widespread), *Annona* (in other adjacent communities), *Bactris*, *Cyperus*, *Euterpe*, *Ficus*, *Ludwigia*, *Mauritia* palm swamps, *Virola*.

Aquatic—*Botryococcus*, *Pediastrum*, *Azolla*, *Ceratopteris*, *Pachira*.

Lowland Neotropical rain forest—This is the prominent community throughout the assemblages, and virtually all other taxa listed in Table 7.2 for the floras are members of the rain forest and the lower elevation phases of the lower to upper montane broad-leaved forest (abundant ferns, *Amanoa*, Bombacaceae [*Catostemma*, *Quararibea*], *Crudia* type, *Humiria*, *Licania*, *Pouteria*). There is a Miocene fauna of freshwater bivalves from the Amazon Basin in northeastern Peru. They are from the MCO at ~16 Ma and show seasonal oxygen isotope variation in growth bands resulting from the annual migration of the ITCZ. According to Kaandrop et al. (2005), "The implications are that humid climate conditions sufficient to sustain a rainforest ecosystem already existed at ~16 Ma ago."

Lower to upper montane broad-leaved forest—Only representatives from the lower elevations of this plant formation are present and include such taxa as *Selaginella*, *Pteris*, *Podocarpus*, *Alchornea*, *Amanoa*, *Hedyosmum*, and *Ilex*. There are no members from the cloud or elfin forest, or northern temperate elements of a temperate deciduous forest association, and no evidence for tundra, or for higher elevation coniferous forest, ceja, or páramo.

According to Hoorn (1994a, p. 53), an expanded version of the modern várzeas of the upper Amazon Basin is probably the closest analog for the middle to late Miocene vegetation and environment. A reconstruction of this setting is shown in Fig. 7.97. Similar communities persisted throughout the Miocene and this allows another aspect of the paleoenvironment to be considered. As noted previously, there was a general global trend toward cooling, drying, and greater seasonality beginning at the end of the early Miocene as a consequence of declining ocean water temperatures. The effects are most evident at the higher northern and southern latitudes (I: pp. 28–29). In the Neotropics, one result was the appearance and spread of tropical grasslands and savannas. Because these plant formations are not evident in assemblages from the western Amazon Basin, Hoorn (1994a, p. 77) concludes that this trend did not affect the vegetation of the region in the Miocene. In contrast, the faunal evidence and the limited paleobotanical data from Argentina for this period suggest the climate was becoming cooler, drier, and more seasonal, and that floras from the Chiquimil, Palo Pintado, and Barranca Final formations show an increase in *Ephedra*, grass, chenoam, and Asteraceae pollen and seasonally dry conditions. The results illustrate the marked difference evident by the Neogene in climate and vegetation between southern cold temperate and northern tropical South America.

The changing paleodrainage in the Amazon Basin is evident from the shifting mosaic of the communities shown in Fig. 7.97, and by the sedimentology. The course (but not the direction) of the Amazon River system is defined by folds in the Precambrian shields; the Orinoco River Basin was defined after the uplift of the Northern Andes in the Late Tertiary. Through the early Miocene, the Guayana Shield was the principal source of sediment for the northwestern Amazon Basin. As the Eastern Cordillera of the Northern Andes Mountains increased in elevation, two changes occurred. One is that the Andes Mountains became the principal source of sediments for the basin. The other is that the basin was tilted sufficiently eastward that the flow of the Amazon River was reversed from west into the Pacific Ocean to east into the Atlantic Ocean. The palynological, faunal, and some sedimentological records place the time of this early phase of uplift and the beginning of modern drainage patterns in the Amazon Basin in about the middle Miocene, while Campbell et al. (2006) believe the current patterns were established later at ~2.5 Ma.

The nature of the marine incursions into the Amazon Basin can be further refined by data from Miocene fish faunas from the Solimões–Pebas formations. These faunas are good indicators of both inundation and the fresh versus brackish-marine nature of the water (Monsch, 1998). It has been proposed that marine encroachments, rather than being episodic, had extended more or less continuously across the entire basin, suggesting connections between the Atlantic–Caribbean and

the Pacific Ocean (Räsänen et al., 1995). The ichthyofauna reveals repeated incursions, separated by intervals of freshwater, a pattern persisting until the late Miocene and one consistent with the changing patterns of mangrove abundance. "The ichthyofaunas also indicate a warm climate, as well as shallow and possibly torrential waters" (Monsch, 1998, p. 31).

Other details of the paleodrainage across Amazonia are revealed by freshwater vertebrate faunas (Díaz de Gamero, 1996). The Urumaco Formation in the Falcón Basin, east of the Maracaibo Basin, is of late Miocene age and is part of a sequence that allows tracing the general course of the paleo-Orinoco River system. In the middle Eocene, the Misoa Delta formed in the Maracaibo Basin at the mouth of a large river that flowed north and drained the Cordillera Central of Colombia and the Guayana Highlands. Western Venezuela was uplifted slightly in the late middle Eocene and delta-building shifted to the south as shown by deposition of the late Eocene to Oligocene deltaic Carbonera Formation in Los Llanos region of Colombia and Venezuela. In the early and middle Miocene, deposition of deltaic deposits shifted eastward to the Falcón Basin. The vertebrate fauna of the Urumaco Formation lies above these deposits, and the sediments, as well as the composition of the fauna, indicate that the Carbonera and Urumaco deltas were all part of the meandering proto-Orinoco River. In the late middle Miocene, further uplift in the Eastern Cordillera caused an eastward shift in the course of the river to its present position. The above scenario has been challenged by Rossetti et al. (2005), who suggest that structural arches in the basins are of little importance to present-day distributions and diversity, and that much of the surface modernization took place within the past 40 Kyr B.P. Irion et al. (2005) believe these interpretations are due to faulty ^{14}C dates contaminated by groundwater and/or soil organic matter.

The question may be raised as to why paleodrainage patterns should be of interest to those concerned with the modern flora and fauna of the region. The answer is that they, like the geomorphic structures discussed in Chapter 2, are ways by which the biota of the basins have been variously and frequently partitioned in the past. As observed early by Wallace (1849) in his riverine hypothesis and more recently by Da Silva and Patton (1993) with reference to the Iquitos Arch, the fragmentation, isolation, and reassembly of populations are the results of historical factors that make for a dynamic Neotropical biota and contribute toward an explanation for its high species diversity (Chapter 8).

The development of vegetation in the then low-lying Bogotá Basin from the Miocene into the Pliocene involved a change from lowland communities of predominantly mangrove, swamp, aquatic, and rain forest communities, like those in the Miocene of the Solimões and Amazonas basins, to ones supplemented by increasing representation from drier shrubland, higher montane broad-leaved forest, and shrubby páramo. This reflects continuing uplift until, by the Pliocene, the Eastern Cordillera had reached a height such that it (1) constituted a barrier to rainfall from the east and resulted in communities of drier aspect to the west, (2) allowed development of an ultra-wet Colombian Chocó vegetation as moisture-laden winds began moving up the newly formed highlands, and (3) provided habitats for formation of páramo vegetation that begins to appear in the Northern Andes Mountains in the Pliocene. The diversity, sequence, number, and ages of the fossil floras in the region, together with careful reference of the fossil specimens to modern taxa, and the associated geological and faunal evidence, have allowed the paleo-component of these ecosystems to be reconstructed in greater detail than is usually possible for the Neotropics. It has further allowed the timing of the uplift of the Andes Mountains to be determined with relative precision.

QUATERNARY (~2.6 MA–PRESENT)

By the Quaternary, all plant formations and associations, virtually all genera, and most modern species were in existence, but they would continue an endless recombination into assemblages varying in composition and distribution. Recovery from the latest of these reshufflings is still ongoing, and this has two implications for Quaternary vegetation history. One, with reference to the modern analog method, is that where an organism does occur is not always the same as where it can occur; viz., it simply may not have had time to expand into the full range of its ecological tolerance. The other is that continuing readjustments in the range of organisms to previous environments diminishes the need for proposed changes in the ecological tolerance of a species through time. Ecological stasis is a surprisingly common characteristic of organisms (DiMichele et al., 2004; Jackson & Erwin, 2006). At least it is common enough that significant differences in ecological tolerances between past and present representatives of a lineage as, for example, in *Ephedra* or *Rhizophora* should not be invoked casually.

The pace of climate and vegetation changes in the Quaternary seems quicker than in the Tertiary because of better resolution, and probably was due in part to slowing plate movement, which reduced the overriding effect of atmospheric CO_2 concentration. This allowed faster-paced events to be more readily expressed, such as the Milankovitch variations on cycles of 100,000 years, 41,000 years, and 23,000 years. There was also an overall increase in land surface from continuing orogeny, periodically augmented during the interglacials by lower sea levels and water tables; generally greater continentality; fluctuating albedo (reflectivity) from changes in vegetation and snow cover; changing CO_2 concentrations through pumps and sinks; erosion of carbonate and silicate rocks; and an immensely complex system of feedbacks that amplified, reduced, cancelled, or reversed the effects of individual factors. As glaciers appeared, expanded, retreated, and disappeared, there were further changes in ocean circulation and thermal stratification from fluctuations in marine temperatures and salinity concentrations, and from the emergence and submergence of land bridges. Atmospheric circulation was altered through the elevation of continental ice sheets up to one mile thick in

the north polar regions (I: pp. 275–278). Adjustments in these delicately balanced complexities resulted in even faster-paced cycles of several to a few thousand years (Heinrich events), and several to a few hundred years (D–O events; I: p. 40). Heinrich events were originally recognized from the North Atlantic Ocean, but they are now known to be reflected in biotic changes in Florida (Grimm et al., 1993) and probably in Brazil and on the Altiplano of Bolivia (see below, this chapter). Both the Younger Dryas and Little Ice Age cold intervals are known from the last deglaciation in South America, and there was a widespread middle Holocene warm period. If these fluctuations characterized the last major glacial–interglacial cycle dating back ~100,000 years, they likely affected vegetation during each of the 18–20 cycles of the ~2.6 Ma of the Quaternary period.

In recounting vegetation changes in Latin America for the Quaternary, it may seem that the discussions of the pollen sequences are more detailed than is necessary for a general summary. The reason is that if similar and contemporaneous short-term fluctuations are detected at several separate localities, they indicate that the forcing mechanisms noted above (e.g., Younger Dryas) were operative across the region. These mechanisms can then be considered likely for sites where information is meager or lacking, and provide a context for inferring patterns of vegetation response as part of a general summary. They also offer paleobotanical support from the terrestrial environment for the extent of rapid, short-term climatic changes detected or suspected in ice and marine cores.

Evidence for Quaternary climatic changes in the Neotropics—It was assumed through about the 1980s that factors causing the climatic and biotic changes so evident in the higher latitudes waned toward the equator, so that both environments and biotas were relatively stable through long periods of geologic time (Chapter 8). The assumption was based on a number of factors, including the general observation that extremes of climate did decrease toward the lower latitudes. These early impressions of stability found support when publications of the CLIMAP Project Members (1976, 1981, 1984) and COHMAP Members (1988) indicated changes of only 0°–2° C at the lower latitudes during the ice ages. However, Emiliani (1955) had already proposed that 60% of the isotopic variation in marine waters at the low latitudes was due to temperature, and he estimated a ~6° C lowering of MAT at the LGM. Then Guilderson et al. (1994) suggested a ~5° C cooling at 19,000 years B.P. based on oxygen isotope and Sr-Ca thermography from corals on Barbados. For the terrestrial environment, Webster and Streten (1978) noted that snow line changes in tropical Australasia were not compatible with the SST reconstructions of CLIMAP, and studies from the High Plain of Bogotá at ~5°N revealed a significant depression of snow line and cooling temperatures at the LGM that were suspected to have extended into the tropical lowlands (see below, this chapter).

A comprehensive review of South American Quaternary geology and geomorphology was made by C. M. Clapperton (1993). That summary discussed the following evidence for significant climatic, tectonic, and environment-altering events in the Andes Mountains, the lowland basins, and in the plains of southern South America:

1. Ponding from Quaternary tectonic movement (uplift, landslides, lava flows) in the Pastaza-Marañon Basin in Amazonian Peru and adjacent western Brazil (inundated each year over an area of ~70,000 km^2), uplift and burial of the Iquitos Arch along the eastern margin of the basin, and subsidence of the basin floor;
2. Re-interpretation of the uniformity of sediments of the "terra firme" (land mostly east of the Iquitos Arch and not annually flooded) deposited in ancient Belterra Lake during the early Pleistocene. This uniformity implied a relatively constant depositional setting (Sombroeck, 1966). More recent views are that these deposits are heterogeneous in origin and age and cannot be used as evidence of environmental stability (Räsänen, 1991; Räsänen et al., 1992);
3. Sedimentary evidence for repeated wet and dry periods within the Mesa Formation of Los Llanos of the Orinoco River Basin (isotope stages 13–9, Yarmouth interglacial of North America; ~475–300 Kyr B.P.);
4. A complex of factors affecting the Amazon Basin during the Quaternary, summarized by Clapperton (1993, pp. 148–151) as evidence for an overall reduction in precipitation, greater seasonality in rainfall, eustatic lowering of sea level of 25–130 m (during each glacial maximum), and a reduction in vegetation cover;
5. Uplift of the Sierra Nevada de Santa Marta and the Cordillera de Mérida at an estimated rate of 4 mm/yr, or 2000 m during the past 500,000 years. The present lower limit of glaciers is at 5000 m (~4000 m at glacial maximum), meaning that few glaciers were present prior to the late Quaternary;
6. Relict Quaternary dunes and eroded hollows in the humid Pantanal implying (a) periodic climates so dry that the protective vegetation cover was significantly reduced, and (b) stronger winds than at present further contributing to desiccation;
7. Development of sand and loess Pampas plains younger than 2.5 Ma under changing climates during the late Cenozoic (Ameghino [1876], dry conditions of a "true Sahara"; Frenguelli [1957], pluvial [wet] and interpluvial [arid] conditions);
8. Eight sedimentary formations and depositional environments of Quaternary age in the Entre Ríos region (Paraná Basin; Irionodo, 1980): Ituziango (Plio–Pleistocene, warm, humid), Salto Chico (middle to early Pleistocene, wet, flooding), Alvear (middle Pleistocene, arid), Hernandarias (middle Pleistocene, wet, marshy), El Palmar (late Pleistocene, warm and humid), Tezanos Pinto (late Pleistocene, arid), La Picada (early Holocene, dry), Los Conquistadores (late Holocene, alternating dry, humid); and
9. Origin of some bajos (enclosed, often water-filled basins)

of Patagonia, beyond the limits of glaciation, by erosion during cold intervals when vegetation was reduced.

Chapter 2 discusses additional evidence for Quaternary tectonism, glaciation, sea-level changes, and climates from the High Andes Mountains and the lowland basins of South America, and this and other data are summarized below:

1. Erosion terraces 30 to 180 m above present sea level in the Amazon Basin and adjacent regions (e.g., on Marajó Island, Brazil), from higher sea levels (~120 m) and lower land surfaces. Clapperton (1993, p. 590), citing the frequent relationship between cooling and drying in the lowlands, suggests this occurred "during Quaternary cold intervals, when climate in this region became drier";
2. Terminal moraines from the last glacial interval in the Cordillera de Mérida (Venezuela) offset through faulting by several tens of meters during the Holocene;
3. Uplift of the Sierra de Perijá (Colombia–Venezuela border) at a rate of 11–16 mm/yr during the Quaternary;
4. Uplift of blocks within the Ecuadorian Andes Mountains by ~150 m within the past 7000 years;
5. Fluctuations in the abundance of mylodonts and equids in the Pleistocene aeolian Cangahua Formation of Ecuador correlated with cold-dry intervals;
6. Evidence for extensive glaciation in the Eastern Cordillera of Bolivia in the form of moraines, tillites, and hummocky surfaces;
7. Alluvial fans in the Gran Chaco (Argentina, eastern Bolivia, southeastern Brazil) originating during humid phases of the Pliocene and Quaternary, and dunes and loess originating during dry conditions correlated with cold phases of the various glacial maxima;
8. Plio–Pleistocene deposits near Antofagasta, Chile, elevated by 240 mm/Kyr within the past 330 Kyr, a 7.8-magnitude earthquake in northern Chile 30 July 1995, and volcanism within the past 930 Kyr along the coast of central Chile;
9. Aeolian deposits (dry conditions) in the Hernandarias Formation of the Entre Ríos region of Argentina dated at 1.3–0.8 Ma, and representing rainfall 13% of the present or ~100–150 mm/yr;
10. Evidence of glaciation in presently ice-free areas of southern Chile, Patagonia, and Tierra del Fuego;
11. Loess sediments (dry conditions) alternating with swamp deposits in the Rosario Formation of the Pampean region of Argentina, dated at 0.73 Ma;
12. Snow line depressions at the LGM estimated at 200–300 m in the Junín region, Peru; 600 m at Laguna Kollpa Kkota, Bolivia; and 1100–1350 m in the Cordillera Oriental, Peru (Smith et al., 2005b);
13. A review of the human history of southern South America, extending to northern Argentina and adjacent southern Brazil, revealing that populations were significantly affected by a middle Holocene dry period (Zárate et al., 2005); and
14. Causal mechanisms for dry periods on the Altiplano link these intervals with intervals of dryness in the Amazon Basin and reduced transport of moisture (Chapter 7).

Although the paleobotanical database for the Quaternary is considerable for certain regions of South America (Tables 7.5, 7.6), the overall history of terrestrial environments and communities still must be anticipated from trends already in motion in the late Neogene and extrapolated from records, mostly for the Late Glacial and Holocene, which become fewer and more discontinuous for older glacial and interglacial times. Much of the evidence is synthesized from separate basins with independent tectonic histories that could affect drainage and vegetation as discussed for the Transvolcanic Belt of Mexico. Thus, the ancillary data summarized above are important because they allow for the expectations that (a) climatic changes initially known from polar regions of the Northern Hemisphere affected the biotas of the Neotropics, (b) these changes fluctuated throughout Quaternary time, (c) they were driven in part by CO_2 levels–ocean circulation–orogeny and were similar but on a finer scale between the northern and southern latitudes as those of the Tertiary (Moran et al., 2006; e.g., the LPTM–EECL, but see Edgar et al., 2007), (d) there was a more evident Milankovitch component, with CO_2 overlay, and climates were often asynchronous between the high northern and southern latitudes in the Quaternary, (e) in the Quaternary, they were generally synchronous from the high northern latitudes to about the Northern Andes, (f) they were transitional and especially complex in the Central Andes, (g) during cold periods, the lowlands and mid-altitudes were often dry, and during warm periods, they were often moist, although variations in the position of the ITCZ complicate the pattern, (h) habitats followed a similar sequence allowing for local influences of slope, exposure, soil, and—particularly important for fine-tuning correlations between events—lag times between marine and terrestrial chronologies, and (i) the lowland vegetation responded in a pattern similar to that of the climate history, with dry plant formations expanding during cold-cooling intervals that were dry or drying, and mesic to wet plant formations expanding during warm-warming intervals that were moist or becoming more moist.

In addition, several broader questions fundamental to the history of Neotropical vegetation can also be addressed through the collective evidence and new methodologies. One is how long recently intensified tectonic and climatic events have been affecting the high-altitude biotas of South America. Each subsequent glaciation destroys much of the evidence of previous ones, and the rise of separate mountain sectors through cycles of volcanism, or the uplift of individual blocks through plate collision and subduction, is often different. Thus, the history of mountain building throughout the Andes Mountains is not uniform. An early conclusion was that very high elevations necessary for the formation of glaciers in South America were attained only in the last ~18,000 years. This view has changed, and Garner's (1975) suggestion that glaciation in the Southern

Andes Mountains may have occurred as early as the latest Miocene is finding support. The earliest glaciation was in Patagonia where tills occur beneath basalts that range in age from late Miocene to Quaternary, and other deposits of glacial origin date from ~3.5 Ma (late Pliocene). The pattern is overlapping, and it is far from simple, but the trend seems to be for glaciation first in Patagonia in the late Miocene (closest to the polar regions, earliest uplift, but to lower elevation), then in the Central Andes Mountains in the late Miocene to Pliocene (Clapperton, 1979; slightly later uplift, but to maximum elevations), and in the Northern Andes Mountains in the Plio–Pleistocene (later uplift to intermediate elevations).

Another general question is: When did the Andes Mountains rise to sufficient heights to constitute a vicariance event and separate lineages into eastern and western populations? By now it is evident that the Andes Mountains are a very complex system. They extend 8000 km and consist of segments uplifted at different times to different heights during the Neogene (Miocene and Pliocene) and Quaternary. There are also passages through the mountains that have allowed crossings at different times. The lowest is the Huancabamba Valley (~2000 m) of the Río Chamaya, northern Peru (Weigend, 2002). As a broad generalization, the Andes Mountains probably achieved about one-half of their average and highest elevations (~1000 and 2000 m) between the early and late Miocene (23–11 Ma), the remaining 2000 m in Mio–Pliocene and Quaternary times, and with a few scattered passages available throughout the intervals. Specialists in the various plant groups know best the dispersal potential and ecological parameters of individual lineages, and whether they were likely in existence at the time and place of a relevant vicariant event.

The varied sources of ancillary evidence for significant climatic change in the middle latitudes include:

1. Oxygen isotope values in the foraminifera *Globigerinoides sacculifer* from off the northern coast of Brazil indicating that marine temperatures were colder than earlier interpreted from CLIMAP data (Wolff et al., 1998);
2. Sediments with titanium (Haug et al., 2001, 2003), iron (Lamy et al., 2004), leaf waxes (Hughen et al., 2004), and isotope values in a core from the same region that show sub-Milankovitch changes correlated with Heinrich and D–O events in the North Atlantic Ocean (Arz et al., 1998);
3. Noble gases in ^{14}C-dated groundwater from a Brazilian aquifer indicating a cooling of >5° C during the LGM (Aeschbach-Hertig et al., 2000);
4. Alkenones from coccolithophorid algae (Bard et al., 1997; see Ohkouchi et al., 2002, for discussion of the strengths and limitations of the technique);
5. Goethite and hematite (terrigenous minerals) consistently peaking during the transition from glacial (dry) to interglacial (moist) periods (Harris & Mix, 1999);
6. Dust and atmospheric gases in varved (annually layered) ice cores;
7. Oxygen isotope composition of planktonic foraminifera within a region of Amazon River discharge (ODP Site 942; 5°45'N, 49°6'W), northern Brazil, showing extremely dry conditions during the Younger Dryas with flow, reduced by an estimated 40% (Maslin & Burns, 2000);
8. Uranium/thorium-dated oxygen isotope record from stalagmites in Botuverá, southeastern Brazil (27°13'S, 49°09'W; 230 m elevation), showing evidence of D–O cycles in precipitation (Cruz et al., 2005); and
9. Amino acid racemization in radiocarbon-dated emu eggshell fragments reflecting global cooling in the Southern Hemisphere (Miller et al., 1997).

There is the potential for estimating Holocene precipitation fluctuations from the growth of speleothems (stalagmite) concretions that in section are similar in appearance to growth rings used in dendrochronology (Bertaux et al., 2002, e.g., figs. 3, 6, 7, 8, 9, 11). Speleothems obtained from João Arruda Cave, Mato Grosso do Sul in central-western Brazil, show evidence for increasing rainfall for the past 3800 years from previous lows. Satellite images show the present extent of glaciers in South America (Williams & Ferrigno, 1998), and other images of the Amazon Basin show innumerable "shadows" of former drainage patterns such as filled oxbow lakes, old channels, and levees now covered by vegetation.

Collectively, this information provides a background for tracing the Quaternary history of South American vegetation and environments. The task is daunting, but the arsenal of new, imaginative techniques is impressive. If the older intuitive-based bias about vegetation history in the Neotropics, based on misconceptions of plate tectonics and terra firme, was that environments and biotas were stable through long periods of geologic time, the current data-based bias from geological and related studies is that the biotas, including those of the tropical lowlands, changed dramatically throughout the Quaternary. The evidence has further shown that the climate-forcing events do not always originate in the immediate vicinity of the Neotropics.

Teleconnections (Markgraf, 2001)—Climates are determined by broadly operating processes such as the Milankovitch variations and CO_2 concentrations, and by a myriad of regional and local events such as the rise and fall of mountain ranges and the opening and closing of land bridges. Teleconnections are the means whereby these climate-forcing mechanisms are transmitted through the global system. The term encompasses the concept that climates are interconnected primarily through the ocean transport of heat and the atmospheric transport of moisture. An example is the cooling at the LGM, which was most intense at the polar extremes, but lowered SST around Barbados by ~5° C due to changes in the heat transfer by the Argulas (Southern Hemisphere)–Gulf Stream (Northern Hemisphere) currents (Guilderson et al., 1994; I: p. 34). Another is the effect of equatorial Pacific ENSO events on the global climate (Dettinger et al., 2001).

The timing and intensity of teleconnected events differ between regions depending on the nature and extent of the

change at the principal source area (cooling at the poles in the Pleistocene, warming at the equator at the LPTM–EECL), the vector (atmospheric, ocean currents), pace of the transfer, and conditions along the pathway and at the terminal sites. The Northern and Southern Hemispheres are alternately tilted toward and away from the sun, so the shorter climate changes influenced by the Milankovitch variations should be reciprocal (asynchronous) at the two poles, and although this is not consistently evident in the records (Blunier et al., 1998; Steig et al., 1998; Steig, 2006), it is the general pattern preserved in the Greenland and Antarctic ice cores. In addition to patterns in the cores themselves, asynchrony in shorter, warm-cold, see-saw events controlled by ocean circulation is shown by Heinrich events (cold) in the North Atlantic Ocean, and by increased algal productivity (warmth) in the Southern Ocean. Sachs and Anderson (2005) used molecular fingerprints based on alkenones from coccolithophorid algae, and brassicosterol from diatoms, together with radioisotope tracers of sedimentation, to identify eight episodes of peak algal growth suggesting intervals of warmth in the southern oceans between 70 and 10 Kyr ago. These corresponded to seven Heinrich and the Younger Dryas cold events in the northern ocean. The differences may also involve upwelling due to reorganization of southern deep-water production.

In the terrestrial environment, climate changes between the northern and the equatorial latitudes are generally synchronous (Genthon et al., 1987; Curry & Oppo, 1997; Lea et al., 2003; Cariaco Basin and Greenland Ice Sheet Project 2), although local variations from advected moisture carried up the eastern slopes of the Andes Mountains, and from dry air carried up the western slopes, can complicate the pattern (Jennerjahn et al., 2004). Some inconsistencies were resolved when lag times were recognized between rapidly changing climates near the end of the last deglaciation at 15–10 Kyr and the vegetation response. The studies were based on leaf waxes washed into the Cariaco Basin off the coast of Venezuela (Hughen et al., 2004). In another study from the equatorial region, removed from the direct effects of continental ice sheets, SSTs from the Cocos Ridge showed a close parallel between temperatures and atmospheric CO_2 on a 100-Kyr cycle (Lea, 2004). Some synchronization is likely imparted by the overriding effect of CO_2 (Medina-Elizalde & Lea, 2005; David Lea, pers. comm., 2005).

A complication in the far Southern Hemisphere is that there is greater synchrony between some terrestrial records and events in the North Atlantic region than with local marine SSTs. Pollen records from the Lake District of southern Chile at 13–9.8 ^{14}C years B.P. show changes that are off-cycle from adjacent marine SST records, and more similar in timing to those of the Northern Hemisphere (Moreno et al., 2001). The different timing with the SST record, and the apparent similarity with events to the north, is attributed to the lag time between cold episodes recorded first in the SST data, and later by glacial and vegetation response. Lamy et al. (2004) present other evidence from iron concentrations in marine sediments off the coast of Chile (a reflection of terrestrial input from glacial activity) that the Antarctic and Patagonian glacial histories are synchronous. A more unified model is slowly being developed, but understanding the interactions between terrestrial and marine temperatures, glacial and vegetation histories, and the timing of Northern and Southern Hemisphere events and when and how these events are expressed in the transitional region of the Central Andes Mountains, as well as discovering the causal factors, are among the most complex of modern scientific endeavors. As noted earlier (I: pp. 39–40):

> "Witnessing the debates and the fine-tuning of significant unifying concepts imparts to each period of science its own uniqueness and special importance. Emerging data from ice cores and refinements in the orbital theory of glaciations are among those that mark this period. It is a challenging and fascinating time to be contemplating Earth history and biotic response because existing technologies are being pushed to their limits, new methodologies are being developed, and broad answers to immensely complex questions are just being formulated."

The extensive literature on teleconnections now includes evidence for better correlation of glacial and Heinrich events in the northern and equatorial latitudes (Lowell et al., 1995; Vidal et al., 1999); similarities in geomagnetic intensity stacks between the North and South Atlantic oceans (also correlated with Heinrich events; Stoner et al., 2002); the tropics as a source of climatic change via resumption of thermohaline circulation during deglaciation in the North Atlantic Ocean (Hoerling et al., 2001; Knorr & Lohmann, 2003; see special section on paleoclimate in *Science*, Vol. 292, 27 April 2001); high-latitude versus equatorial Pacific Ocean similarity in obliquity forcing (Liu & Herbert, 2004); El Niño-like teleconnections as far north as New England (Rittenour et al., 2000); synchrony of savanna environments to the north and south of the equator in South America (Behling & Hooghiemstra, 2001); links between the Holocene Asian monsoon and North Atlantic climate (Wang et al., 2005); and possible synchrony of climatic events between Africa and the Northern Hemisphere (Johnson et al., 2002), China and Greenland (Kienast et al., 2001), and, in more recent times, between tropical SSTs and the dust bowls of the United States (Schubert et al., 2004). Further literature on teleconnections is given in the Additional References section at the end of this chapter, and summaries are provided by Markgraf (2001; Markgraf et al., 2000). A consequence of the concept of teleconnections is the realization that there is a system whereby the effects of climate-altering factors anywhere in the world, including environmental degradation, are slowly, often imperceptibly, but inevitably transferred to other parts of the globe.

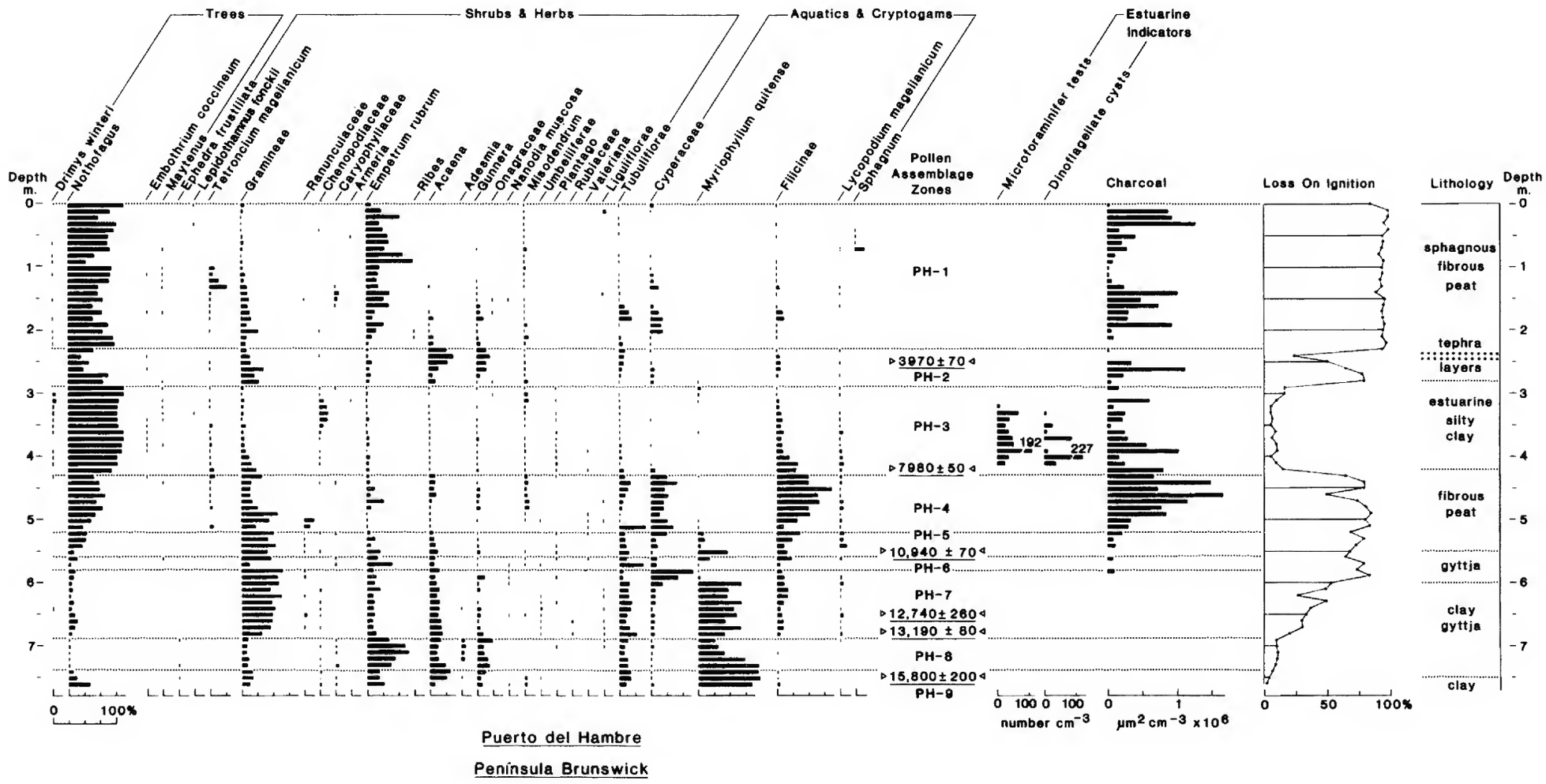


Figure 7.98. Fossil spore and pollen diagram from a mire deposit at Puerto del Hambre, southern Patagonia. Reprinted from Heusser (1995a), with permission of Elsevier Science Publishers, Amsterdam.

Argentina and Chile

Glaciation to the far south in the region of Patagonia, southern Chile, and Tierra del Fuego was probably under way locally by the late Miocene and certainly by the Pliocene. As noted earlier, later advances removed much of the evidence of early glaciations, and the sequence begins with Late Glacial structures and with recovery vegetation preserved in interlobate and Holocene bog and lake deposits. It is a complicated record to read because of the insular environment, complex topography with elevations extending from sea level to ~1000 m on the southern islands and progressively higher northward, an eastern and western region divided by the southward diminishing Andean cordillera, discontinuous coastal mountains, a geologically meandering anticyclone (high pressure) system, some uncertainty about cold reversals during Holocene deglaciation (e.g., a Younger Dryas event), and vegetation involving succession from barren ground superimposed on the effects of climate change. *Nothofagus* pollen is generally present throughout the pollen profiles, and changes in the plant formations are inferred mostly from its quantitative fluctuations, and from variations in the amount of associated shrub, herb, and especially grass pollen. A record of these relatively subtle shifts is preserved in mires adjacent to the Beagle Canal (55°S; Heusser, 1998), and at Punta Arenas (53°09'S) and Torres del Paine (50°59'S) beginning at ~16,000 years B.P. (Heusser, 1995a; Fig. 7.98). In the Late Glacial, there was tundra (*Sphagnum*, Poaceae, *Acaena*, Caryophyllaceae, Cyperaceae, *Empetrum*, *Gunnera*, tubiflorae Asteraceae) indicating a cold-dry climate. In the early Holocene, a grassy steppe (shrubland) developed with *Chiliotrichum*, *Festuca*, *Mulinum*, *Stipa*, and *Verbena* (steppe is primarily a European-Asian term for "temperate shrub vegetation with plentiful short grasses often growing on dry seasonally cold plains and mountain slopes," I: p. 23). *Nothofagus* appeared soon after deglaciation (~14,000 years B.P.), and closed *Nothofagus* forests growing under cool wet climates formed later in the Holocene (~10,000 years B.P.). At the coldest Late Glacial interval, temperatures were 5°–6° C lower than at present, and Markgraf (1993) estimates that MAT was below freezing year round. MAP was <300 mm increasing to ~500–800 mm at the steppe–woodland transition, and there was a ~mid-Holocene dry interval (Mancini et al., 2005). This same interval is recorded in other playa lakes in northern Patagonia (e.g., 47°–39°S; Schäbitz, 1994), suggesting that mid-Holocene dryness was widespread across southern South America. An important control on the climate and biota was the latitudinal displacement of the cold winds of the Antarctic anticyclone (high pressure) system that extended across the southern parts of other Southern Hemisphere continents. At glacial maxima, this system covered an area about double that of the interglacials, it shifted climatic zones northward by ~10°, and there were associated droughts (Iriondo, 1999a). Glacial events indicate a Younger Dryas cold period ~14,000–8500 years B.P. (but see Markgraf, 1991; Bennett et al., 2000) and a Little Ice Age 1300–~1850 C.E. Another factor in the Holocene environment was fire set by the Tierra del Fuego Indians. The earliest human occupation dates from at least 11,000 years B.P. (Rabassa et al., 2000; ~13,000 years B.P., Coronato et al., 1999; before 13,000 years B.P., Heusser, 1994). This is about the same time as in the Central Andes of Argentina (Agua de la Cueva site; Garcia et al., 1999) and in the eastern La Plata

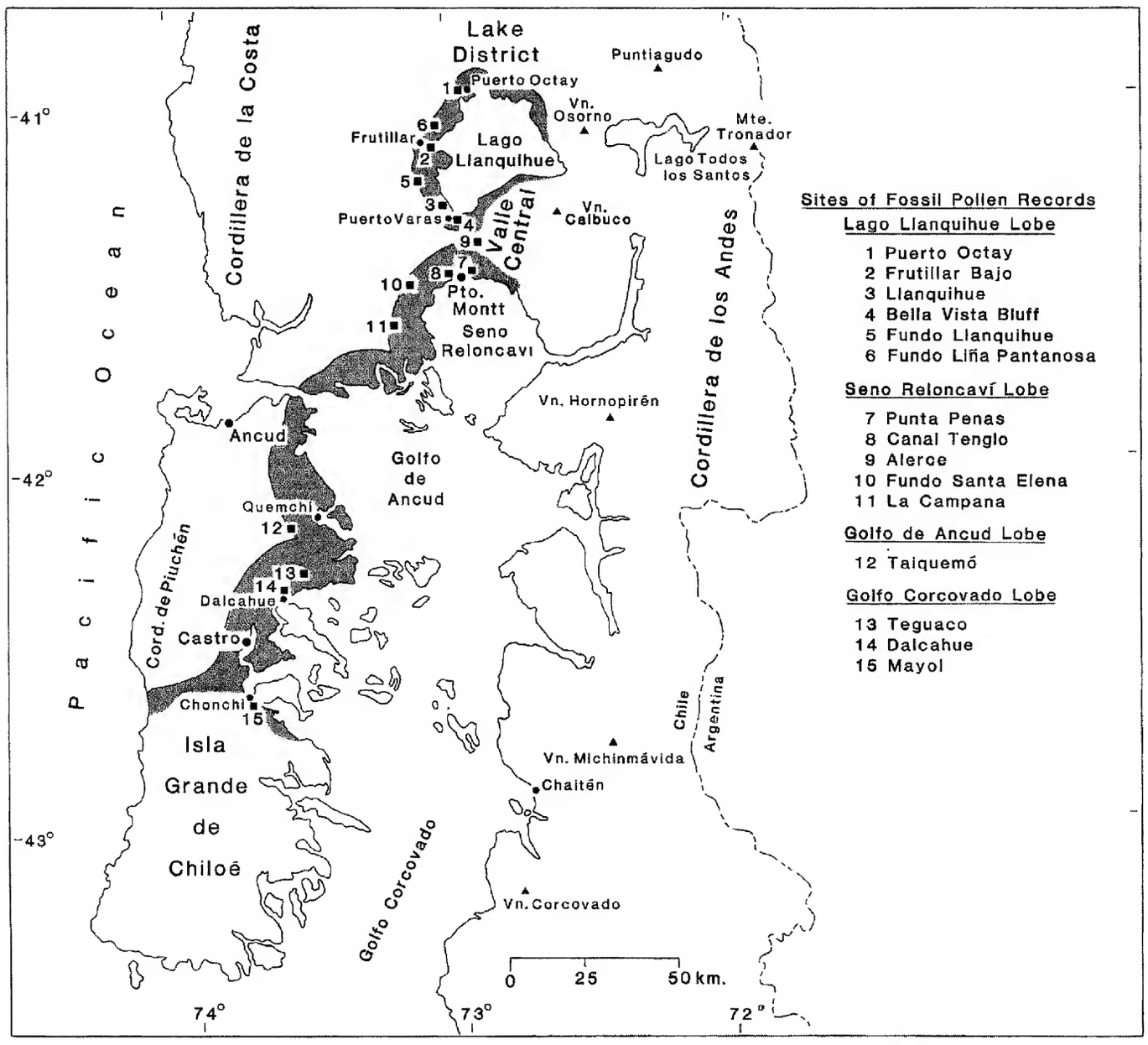


Figure 7.99. Index map of fossil spore and pollen sites and extent of piedmont glacial lobes in the Valle Central, Southern Lake District, Isla Grande de Chiloé, Chile, during the late Llanquihue glaciation. Stippling indicates the extent of glacial drift at the foreland limit. From Heusser et al. (1999). Used with permission of *Geografiska Annaler*, Blackwell Publishing, Oxford, U.K.

Basin (13,000–11,000 years B.P.; Rodriguez, 2005). Other than fire, the impact of the early hunters, mostly of *Llama guanicoe* (Miotti & Salemme, 1999), was not extensive, and evidence of their presence is primarily from increasing charcoal beginning at ~11,000 years B.P. (Fig. 7.98).

A similar vegetation sequence occurs toward the north in Santa Cruz Province (Mancini, 1993, 1998, 2001; Paez et al., 1999; Mancini et al., 2002) and from the eastern grasslands of Buenos Aires Province (35°–40°S). This record includes a cold dry tundra, a more warm humid grassy steppe, shrub steppe with *Nothofagus*, an increase in *Nothofagus* to a more or less closed forest, and intervening local dry-humid fluctuations with shifts between ecotones through the Holocene (see also Iriondo, 1999b; Prieto, 2000; Stutz et al., 2002; Chile: Villagrán M., 1980). Also in the Pampas of Buenos Aires Province, alluvial sequences and malacological and pollen analyses along the Luján River (34°S, 59°W) show moist climates for the past 11 ^{14}C Kyr B.P. (~13 Kyr cal. years) when shallow water, wetlands, and floodplains were expanding (Prieto et al., 2004). Between 9000 and 3000 ^{14}C years B.P., these features contracted, reflecting the mid-Holocene dry interval.

In the Monte region, information on Quaternary vegetation is available from rodent middens, but the picture is not clear. Compared to the North American deserts and the Atacama Desert of Chile, the vegetation was relatively stable, showing little vertical displacement or northern migration at glacial maxima, at least as revealed by midden evidence (Betancourt, 2004). The Sonoran and Chihuahuan deserts were juniper-pine woodlands during the pluvial climates of the cold intervals, but the Monte apparently remained primarily desert. The Puna region of northeastern Argentina was very dry in the middle Holocene (Yacobaccio & Morales, 2005). One reason for the apparent stability may be that the Andes Mountains sheltered the eastern plains and highlands from shifts in the southern westerlies during the Quaternary.

Spore and pollen sequences are available from 15 sites west of the Andes Mountains along the piedmont extending to the Cordillera de la Costa in the Lake District of Chile (~41°–43°S; Isla Grande de Chiloé; Heusser et al., 1999; Figs. 7.99, 7.100). The oldest record is for a glacial advance ~50,000 ^{14}C years B.P. (marine isotope stage 4; cold, dry). The vegetation begins with a cool, humid interstadial (stage 3; 47,000 years B.P.) supporting an evergreen forest of *Nothofagus*, later replaced by a grassy *Nothofagus* parkland with cooling after ~47,000 years B.P. There were subsequent grass and shrub maxima among stands of *Nothofagus* and glacial advances at 22,400 years B.P. and 14,800 years B.P. (marine isotope state 2) with summer temperatures estimated at 6°–8° C below the present. Warming interstadials (by 5°–6° C) at ~14,000 years B.P. led to a closed canopy *Nothofagus* forest by ~12,000 years B.P. There was cooling by an estimated 2°–3° C from 12,000–10,000 years B.P., followed by modern conditions.

In addition to *Nothofagus*, there are two other genera important in the past and present vegetation of southern South America that illustrate the multiplicity of sources being used to refine the history of various ecosystems. *Azolla* is an aquatic

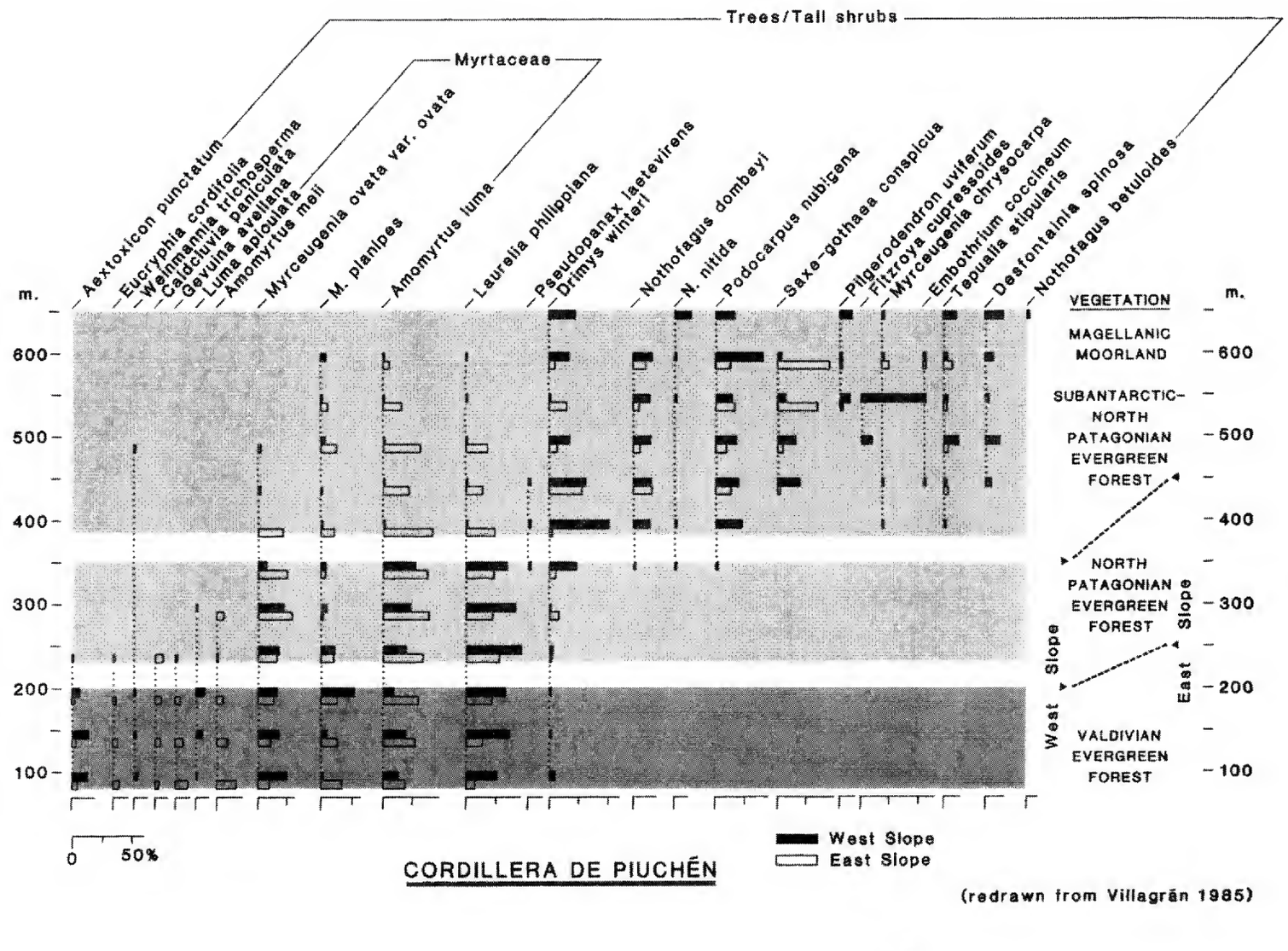


Figure 7.100. Top: Relative abundance of trees and tall shrubs along an E–W transect, Cordillera de Piuchén, Isla Grande de Chiloé, Chile. Middle: Principal plant cover in five communities along a 130-m transect, elevation 700 m, in Magellanic moorland, Cordillera de Piuchén, Isla Grande de Chiloé, Chile. Bottom: Diagram from Puerto Octay, Chile, showing spore and pollen assemblage zones. From Heusser et al. (1999). Used with permission of *Geografiska Annaler*, Blackwell Publishing, Oxford, U.K.

fern known from the Cretaceous onward in South America (Table 7.1) and is found in the Quaternary of southern South America during warm, dry intervals (e.g., at 11,500 and 8900 years B.P.). At present in the Chilotan Archipelago, *Azolla* grows where the mean summer temperature is ~14° C (Heusser et al., 1996), quantifying the temperatures of the warmer periods and, by inference, reflecting the periodic presence of open freshwater communities through the warmer intervals of the Quaternary. The fossils are proving useful elsewhere to test the hypothesis that the warm conditions of the Eocene intensified precipitation in the high latitudes with a freshening of Arctic waters from runoff. Brinkhuis et al. (2006) found large numbers of *Azolla* fossils in cores from the Arctic Basin that grew and reproduced at the beginning of the middle Eocene ~50 Ma, indicating a temperature rise from ~10° to 13° C.

Fitzroya cupressoides (Cupressaceae; Appendix 1.22) is a tree of the *Araucaria* forest that persisted in favorable habitats in Patagonia during the LGM. A question is whether there was a single refugium on ice-free parts of the Chilean coast, or several sites from which *Fitzroya* spread. Isozyme variation was scored for 21 loci from 24 populations across the range of the tree. The populations on the eastern slopes were most variable, with more alleles per locus, a larger number of total alleles, more rare alleles, and higher polymorphism, than populations on the western slopes. The inference is that there were at least two glacial refugia for *Fitzroya cupressoides* (Premoli et al., 2000). Similar evidence was obtained for changing and fragmented populations of *Austrocedrus chilensis* (Cupressaceae; Pastorino & Gallo, 2002).

The geomorphological and paleosol evidence is generally consistent with the record from fossil spores and pollen in that similar shifts in climate, and the timing of these shifts, are evident in the glacial features (Kröhling, 1999). Carignano (1999) summarizes these for the province of Córdoba in Argentina as follows: (1) late Pleistocene—loess deposition, formation of extensive alluvial fans, cold, dry climate; (2) late Pleistocene–Holocene transition—increased fluvial deposition, peat and soil formation, warmer, more humid climates; (3) early Holocene—aeolian sand and loess deposition, colder, drier climate; (4) mid to late Holocene—warmer, humid climates becoming colder and drier toward the Little Ice Age (~1300–1850 C.E.; for southern Chile see Marden, 1997; McCulloch & Bentley, 1998). Farther north in the province of Jujuy, the late Pleistocene was also cold and dry until ~8900 years B.P. (loess beds), followed by a warm, humid hypsithermal interval (8900–6400 years B.P.), a dry interval between 6400 and 1400 years B.P., and the modern humid phase developing after 1400 years B.P. (Alcalde & Kulemeyer, 1999).

There are numerous other geological studies from this classical glacial setting of southern South America that provide much additional information for reconstructing details of the paleoclimate (e.g., Cioccale, 1999; Tonni et al., 1999; Trauth & Strecker, 1999; Zinck & Sayago, 1999, 2001; Gilli et al., 2001). The Quaternary landscape was a dynamic one, and the pace of environmental change and vegetation response was rapid. A summary of these finer-resolution events is provided by Heusser (2003).

It is noteworthy that cooling temperatures were producing tundra climates, and by inference tundra vegetation, in the lowlands of Patagonia and Tierra del Fuego and in scattered sites along the southern and central Andes Mountains from the late Miocene onward. The same temperature trend, in combination with the somewhat later rise in elevation, was creating alpine tundra or páramo in the Northern Andes Mountains in the Pliocene and especially in the Plio–Pleistocene. Thus, throughout Latin America, tundra and páramo are the most recent of the natural plant formations, as further suggested by the close affinities of many modern species with those at lower elevations in the same region (Chapter 3, Colombia).

In central Chile (34°30'S) inland ~80 km, sediments of Laguna de Tagua Tagua provide the following vegetation and precipitation sequence for the past 46,000 years (Valero-Garcés et al., 2005): >43,500–42,400 years B.P. humid; 42,400–40,100 years B.P. drier and cooler; 40,000–21,500 years B.P. humid; 21,000–19,500 years B.P. dry; 19,500–17,000 years B.P. (LGM) humid; 17,000–15,000 years B.P. dry; 13,500–11,500 years B.P. humid. Conditions in the early and middle Holocene (after 11,500 years B.P.) are unsettled for the region (see below), but for Laguna de Tagua Tagua and environs they are interpreted as dry.

In central coastal Chile, the vegetation and climate is known for the past 7500 years from a spore and pollen study at Laguna Aculeo (34°S, 350 m elevation) 50 km southeast of Santiago (Villa-Martínez et al., 2003). Prior to 5700 years B.P., within the mid-Holocene warm period between ~7000 and 5000 years B.P., halophytes were prominent, and it was drier than at present. Between 5700 and 3200 years B.P. it became more humid as shown by the establishment of a freshwater lake, a decrease in halophytes, and an increase in pollen of trees and herbaceous plants. The modern Mediterranean (winter wet) climate of central Chile was present during this interval and, by inference, during all similar intervals for the past 2.6 Ma. From 3200 to 100 years B.P., humid conditions increased with fluctuations indicated by turbidite layers deposited during intervals of torrential rains probably associated with ENSO events. As will be seen later, the latest cycle of regular and periodically intensive ENSO events is known for Peru from ~5800 years B.P.

Atacama Desert—Northern coastal Chile and the adjacent upland, under the South Pacific anticyclone system, is a separate biotic province from southern South America, under the Antarctic anticyclone system, and it supports the continent's only extensive natural desert. Arid conditions result from the orographic deflection of rainfall from the east by the Andes Mountains, and from westerly winds depleted of moisture after crossing the cold Humboldt Current. Plants pre-adapted to local aridity by soil, slope, and exposure probably were present in the Oligo–Miocene as effects of the current were supplemented by the increasing deflection of moisture. The full desert likely began forming in about the middle Miocene as globally cooling ocean waters intensified seasonality. Arid

conditions are documented for northern Chile by the Mio–Pliocene (previous section; Gaupp et al., 1999). The desert was modernized during the Quaternary, varied with a precessional cycle of 23 and 19 Kyr (Stuut & Lamy, 2004), and has fluctuated with El Niño events.

Tracing the history of the desert is constrained by the meager plant material that normally preserves under arid conditions. However, rodent middens constructed by *Abrocoma*, *Lagidium*, *Octodontomys*, and *Phyllotis* from the surrounding vegetation, together with paleoenvironments reconstructed from ancillary lines of geological and other evidence (e.g., diatoms from paleospring deposits), are revealing changes during the Quaternary in the Atacama Desert and in the adjacent western Altiplano. By the LGM at 18 Kyr, sediment analysis and spore and pollen records indicate dry conditions in the Atacama of northern Chile (Grosjean et al., 2001). The contents of fossil middens (Betancourt et al., 2000; Latorre et al., 2003, 2005) suggest moist conditions in the higher Atacama between 16,200 and 10,500 years B.P., with the wettest period being between 11,800 and 10,500 years B.P. MAP is estimated at 70–100 mm at the driest sites at 2600 m, compared to the present MAP of 20 mm. The middens are located between 2400 and 3200 m, many of the plants found in them presently grow above 3800 m (the foraging range of the rodents is ~100 m), and the ground cover of grasses was dense. Sediment analysis also shows moist conditions around this time (after ~12 Kyr, and especially between 11 and 9 Kyr). Additional studies indicate a moderate-sized lake was present elsewhere on the Bolivian Altiplano in the early Holocene until at least 9,500 years B.P. (Sylvestre et al., 1999; see later section on Bolivia, this chapter). According to the midden record, after 10,500 years B.P., the site becomes generally drier until 7,100 years B.P. but moisture regimes fluctuated (e.g., there is a wet phase in the mid-Holocene between 7,100 and 3,500 years B.P.). At this stage, the sequence of regional environments and the biotas are being spliced together from different methodologies and from several different regional sources, a consensus has not yet been achieved, and the complex, multifactor causal mechanisms are not fully known (Grosjean et al., 2003).

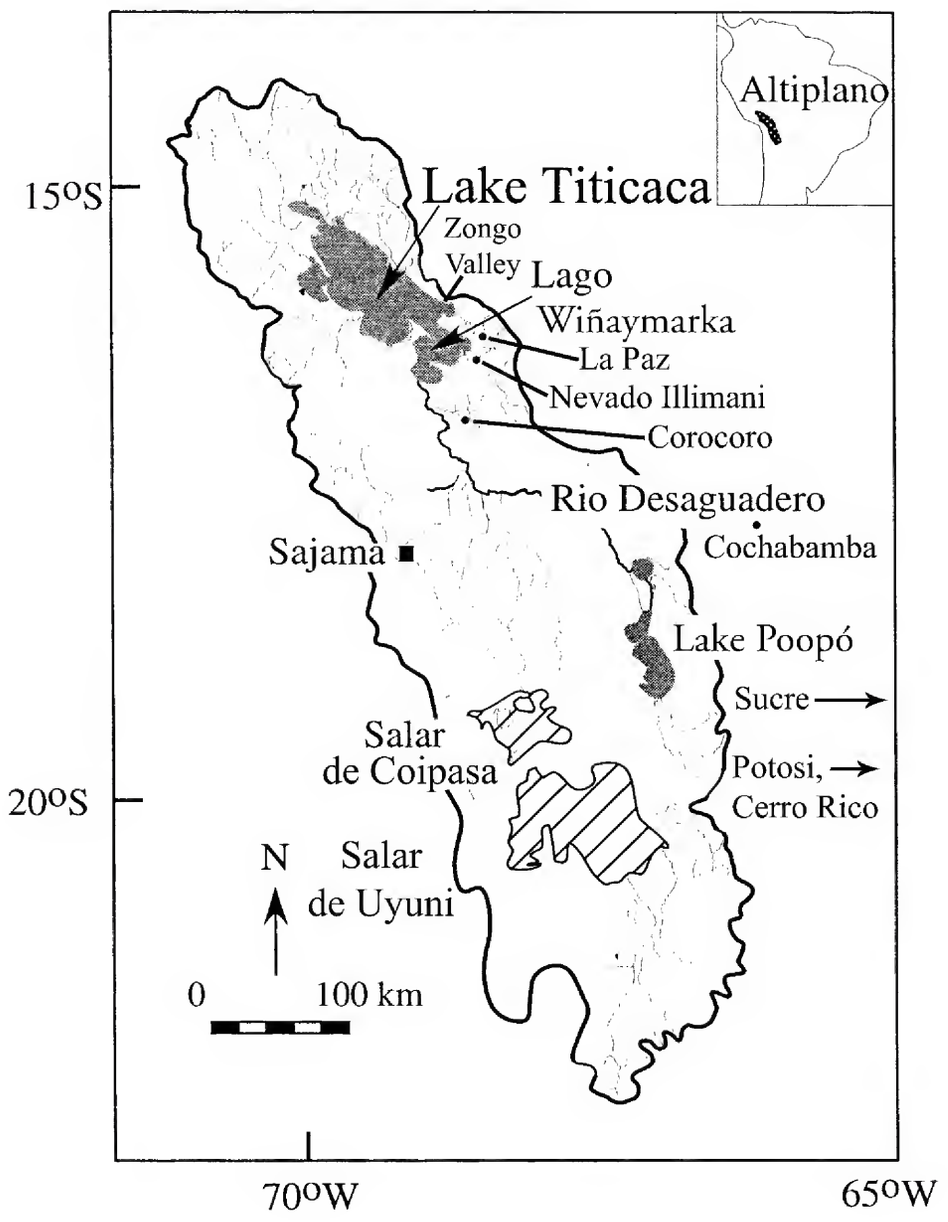


Figure 7.101. Index map of place names in Bolivia mentioned in the text. Based on Paduano et al. (2003) and other sources.

Bolivia

In the lowlands of eastern Bolivia, a 50-Kyr record from the Noel Kempff Mercado National Park is dominated by dry forest and savanna vegetation until a transition phase between 6 and 3 ^{14}C Kyr ago that resulted in present lowland rain forest. Holocene phases indicating greater MAP are consistent with some records from the Altiplano (see below) and suggest greater summertime (wet season) insolation (Burbridge et al., 2004; modern pollen rain see Gosling et al., 2005, and Chapter 8, Refugia).

Altiplano—In contrast to areas where data are limited, the region including the high-Andean parts of Bolivia has become a center for studies on glacial geology, paleoclimates, interhemispheric comparisons of glacial events and chronologies, and global climate change. A detailed sequence is now available for lake cycles from the southern Bolivian Altiplano, supported by 53 new uranium/thorium and 87 new ^{14}C dates (Placzek et al., 2006). The basins are now dry or the lakes oligotrophic, but over the past 120 Kyr, the sediments reveal significant changes in moisture. Between 120 and 98 Kyr, some lakes were ~80 m deep (moist conditions). At 98–18.1 Kyr, there was general intermittent shallowing, as at 95–80, 46, and 24–20.5 Kyr (drier conditions; toward the south, for the period between 40 and 25 Kyr in the Andes Mountains of northwestern Argentina, evidence from enhanced landslide deposits suggests humid conditions; Trauth & Strecker, 1999; Trauth et al., 2003). Then between 18.1 and 14.1 Kyr B.P., there developed "the deepest (~140 m) and largest lake in the basin over the past 120 Kyr" (Placzek et al., 2006), followed by a ~55-m-deep lake between ~13 and 11 Kyr. Various causal factors are cited, including increased moisture during wet intervals in the Amazon Basin transported to the Altiplano by strengthened trade winds or a southern displacement of the ITCZ, but here there is no apparent correlation with a single-season (e.g., January) precessional insolation as suggested for the northern Altiplano (Jay Quade, pers. comm., 2006; see below). To the extent that moisture regimes in Amazonia and the Altiplano are linked, dry intervals on the Altiplano would presumably reflect dry-

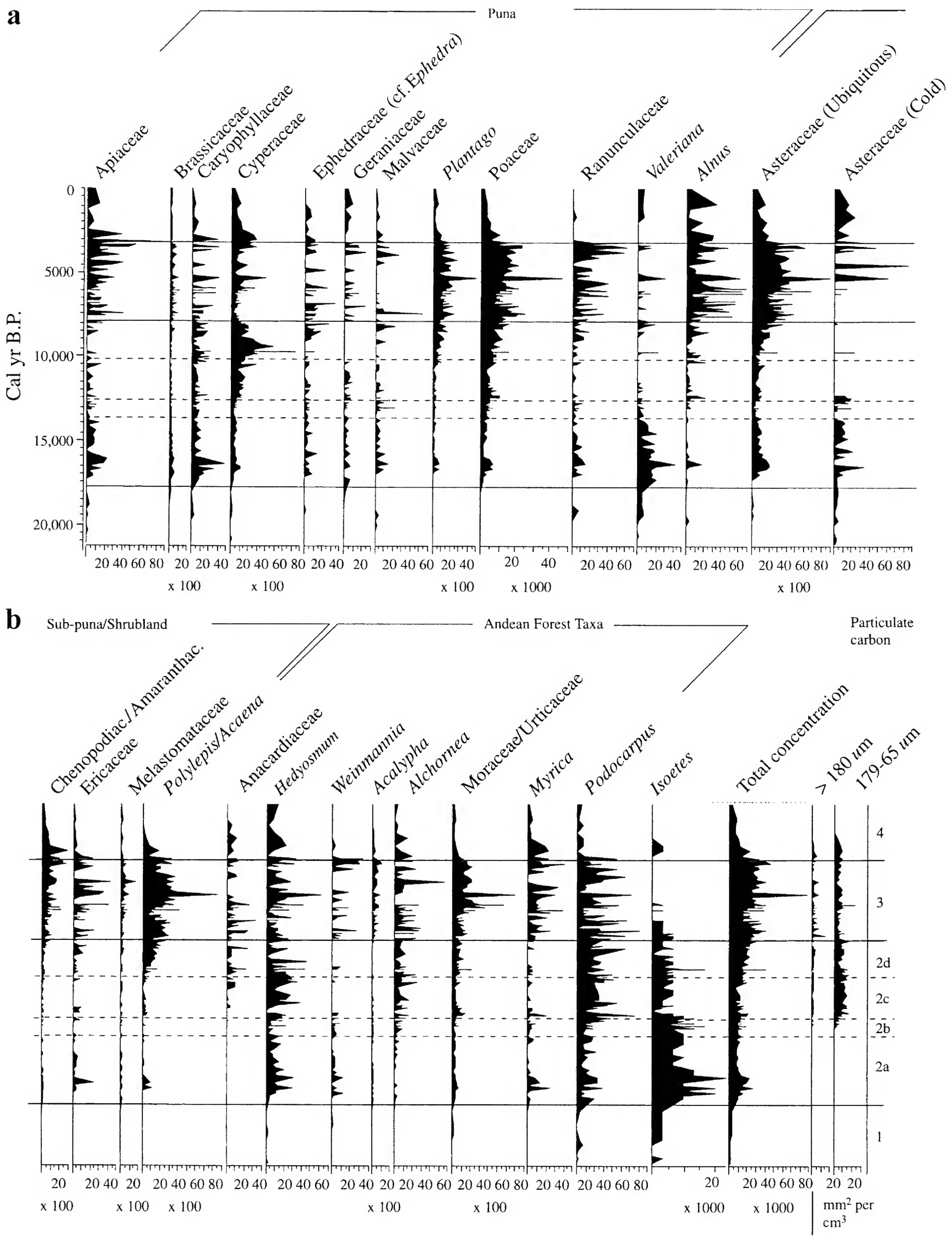


Figure 7.102. Spore and pollen concentration for selected taxa in sediments from Lake Titicaca, Bolivia. Reprinted from Paduano et al. (2003), with permission of Elsevier Science Publishers, Amsterdam.

ness in the Amazon Basin, supporting accumulating evidence that current mesic conditions did not prevail uniformly across the basin throughout the Quaternary.

In the northern Altiplano, there were early studies on Quaternary spores and pollen from the valley of Cochabamba (Graf, 1981a) and Lake Titicaca (Leyden, 1989; Figs. 2.44, 7.101). More recent cores obtained from Lake Titicaca (3810 m) preserve a record of spores, pollen, charcoal (Paduano et al., 2003), and diatoms (Tapia et al., 2003) for the past ~30,000 years B.P. These can be used to describe the sequence of vegetation, to make comparisons with those from the high Atacama and the southern Altiplano, and to illustrate the status of Late Glacial and Holocene investigations on environmental history for the Bolivian highlands (Fig. 7.102). Until 21 Kyr B.P. (Late Glacial), temperatures in the Lake Titicaca Basin were cold (5°–8° C below the present 8° C; 3°–5° C fide Paul Baker, pers. comm., 2005), the snow line extended ~500 m lower than the present 4850 m, and moisture conditions were interpreted as wet. Warming was under way by ~21 Kyr B.P. (Smith et al., 2005b, c), lake levels were high, and the climate continued wet until ~10 Kyr B.P. (early Holocene), with drier intervals between 17.7 and 13.7 Kyr B.P. (Baker et al., 2001b). To explain high lake levels, a process like that described for the lowlands of eastern Bolivia (Burbridge et al., 2004) is proposed for the Altiplano (Baker et al., 2001a). It includes an enhanced SASM (responsible for ~80% of the annual rainfall) induced through (1) peak precessional-period influence on insolation, and (2) possible ocean-atmosphere interactions in the equatorial North Atlantic Ocean that coincide with high-latitude North Atlantic cold intervals such as Heinrich events and D–O cycles. Charcoal increased, especially at 13.7 Kyr B.P., likely due to natural fires as grasses became more abundant. MAT is estimated at 2°–3° C below the present. The interval of deglaciation and high lake levels is earlier here than in the Bølling-Allerød warming in the Northern Hemisphere and earlier than some Andean records (Seltzer et al., 2002). For example, lake levels were falling at this time in the Sabana de Bogotá region. Another difference is that the Lake Titicaca cores suggest no warming corresponding to the Guantiva Interstadial in the Sabana de Bogotá of Colombia (14.7–13 Kyr B.P.). Heine (2000) notes that correlation between the lake levels and glacial cycles requires numerous, accurate age determinations. For Lake Titicaca, the correlation is facilitated by the presence of glacial and lake-level indicators in the same core (Paul Baker, pers. comm., 2005). There is a mid-Holocene dry period between 9000 and ~3100 years B.P. with a peak at 7960–3100 years B.P. (~8000–4300 years B.P., Hanselman et al., 2005; 7900–4500 years B.P., Río Desaguadero Valley, Rigsby et al., 2005) when lake levels dropped by an estimated ~100 m (the lowest level in the 30-Kyr record was at ~5500 years B.P.), it was a time of maximum salinity, charcoal levels increased, and MAT was possibly 1°–3° C warmer than at present. Dry conditions are further suggested by the sediment record between 8000 and 3000 years B.P. (but see Rech et al., 2003), and high levels of dust are present in sections of ice cores from Sajama, Bolivia, dated between 9000 and 3000 years B.P. (Thompson et al., 1998). This is consistent with the middle Holocene dry interval from other sites. It correlates with evidence from glacial geology in the Atacama Desert of Chile and interpretations of the emerging paleobotanical evidence from the Altiplano, but, as noted, not with midden and other evidence that suggests humid conditions, and not with some sedimentary analyses from confluent Lake Wiñaymarka at the south end of Lake Titicaca. Here, cooler conditions are suggested between 8700 and 6500 years B.P. and at 5800 years B.P. (Ybert, 1992). Lake levels began to rise ~4000 years ago and reached modern levels ~1500 years B.P. (Abbott et al., 1997a, b). After 3000 years B.P., the midden evidence from the high Atacama indicates very dry conditions, while the northern Altiplano is interpreted as moist (Baker et al., 2001a, b).

Archeological sites around paleolakes on the Altiplano of northern Chile at elevations around 3600 m and in the Atacama Desert (2976 m) show human occupation generally corresponding to times of moist climates and high lake levels (Grosjean, 1994; Grosjean & Núñez, 1994; Núñez et al., 2002; Grosjean et al., 2005). These conditions prevailed between 13,000 and 9500 years B.P. and after 4500 years B.P., and the MAP is estimated at 400–500 mm. The interval between 9500 and 4500 years B.P. was dry and the sites were abandoned. The inhabitants were primarily hunters of the Pleistocene fauna and had limited effect on the vegetation as revealed by spore and pollen diagrams.

Increases in the pollen of weeds (chenoams, Asteraceae) indicate human disturbance beginning again at ~4000 years B.P. and peaking at 2600 years B.P. Between C.E. 1100 and 1000, the influential Tiwanaku culture on the Altiplano and in the Yungas declined. Ortloff and Kolata (1993) conclude from their reading of the Quelccaya, Peru, ice core record (Thompson et al., 1979, 1982, 1988; Thompson & Moseley-Thompson, 1987, 1989) that the likely cause was environmental deterioration caused by a dry interval between C.E. 1400 and 1000 leading to collapse of the agricultural-based economy, although an alternative interpretation is the occurrence of multiple, shorter decade-long droughts.

Several factors of the physical environment (paleohydrology, tectonics), climate (position of the westerlies, ITCZ), and forcing mechanisms (precessional cycles) are being incorporated into developing models for Altiplano paleoclimates (Grosjean, 1994; Lamy et al., 1998, 1999, 2000; Ortlieb et al., 1996; Rech et al., 2002; Valero-Garcés et al., 1999; Veit, 1996a, b). A Pole–Equator–Pole Initiative (PEPI) workshop on the paleoclimates of the Central Andes was held in Tucson, Arizona (Seltzer, 2001; abstracts are available at http://www.paztcn.wr.usgs.gov/pcaw/), and the papers were published as a special issue of *Palaeogeography, Palaeoclimatology, and Palaeoecology* (Vol. 194, 2003). A number of factors were identified that need to be resolved before agreement is reached on the regional vegetation and climate history. One not discussed extensively in Andean paleoecology is the possibility of subterranean tectonic shifts causing changes in water table, lake levels, patterns

of groundwater distribution and surface drainage, and vegetation independent of climate. This is a factor in the basins of the Transvolcanic Belt of Mexico, and both regions are among the most geologically active in Latin America. Whatever its role may be in the Central Andes, one certainty is that it will not be a simplistic either-or factor, but one operating randomly and with varying intensities within cycles of climatic change and successional patterns of recovery vegetation.

Other uncertainties are caused by differing response times between vegetation, climatic change, and glacial advances and retreats; teleconnection with events elsewhere; and problems associated with ^{14}C dating of carbonate-charged waters (for a discussion of this source of error, see Placzek et al., 2006). As noted by Grosjean et al. (2003), "The question whether the mid-Holocene (between ca. 9 and 4 cal Kyr B.P.) in the Atacama Desert and the Central Andes in general was humid or dry has wide implications with regard to the understanding of long-term climate variability in South America." The results will also be important in eventually integrating forcing mechanisms for the changes in Quaternary vegetation with other parts of Latin America.

Numerous issues remain to be addressed in studies of the northern Altiplano. The plant communities, as read from the spore and pollen diagrams, seem relatively stable (viz., near modern after ~13.7 Kyr B.P.) considering the environmental fluctuations proposed from other lines of evidence. There are difficulties in defining the paleoecological meaning of fluctuations in *Isoetes* spores, and there is uncertainty about the precision with which grass pollen can be separated into paleoecologically distinct groups. The relationship between subtle alterations in vegetation and presumed causal factors such as climate, fire, hydrology, and human disturbance is not fully resolved. Some temperature events of regional or global scope (i.e., the Younger Dryas) are not evident (but possibly expressed as wet periods; Rigsby et al., 2005), and there is earlier deglaciation compared with other regional records. The latter emphasizes again the need for precise dating and stratigraphy when dealing with such rapid events that are compressed into intervals of several hundred to a few thousand years (e.g., 12 distinct wet periods within the last 50,000 years; Rigsby et al., 2005).

All the uncertainties just mentioned attest to the many challenges remaining in constructing an inclusive Quaternary environmental history for the Central Andes (Paduano et al., 2003). Nonetheless, the broad array of techniques is yielding promising results (Clapperton et al., 1997; Mourguiart et al., 1998; Seltzer et al., 1998; Sylvestre et al., 1999; Abbott et al., 2000; Argollo & Mourguiart, 2000; Wolfe et al., 2001; Servant & Servant-Vildary, 2003). For example, the study of cores in the Salar de Uyuni on the Altiplano contributes the fact that moisture regimes may have varied in concert with the ~20 Kyr precessional cycle (but see Placzek et al., 2006) and with Heinrich events 1 and 2 and that there was a Younger Dryas cold interval (Baker et al., 2001a). Results of study of an ice core from the Nevado Illimani (Hoffmann et al., 2003; Ramirez et al., 2003) suggest that here the Late Glacial was in fact cold and wet, and analyses of snow lines in the Western Cordillera of the Central Andes Mountains also indicate increased precipitation during the stadials (Klein et al., 1999). This is consistent with results from Huascarán, Peru (Thompson et al., 1995), and the Salar de Uyuni and further suggests that the dry interval of the Sajama, Bolivia, ice core (Thompson et al., 1998) may reflect local conditions. Elsewhere, glacial climates were cold and dry. As details are being refined, the record, nonetheless, documents a dynamic Quaternary landscape and vegetation in the Altiplano, the high Central Andes generally, and in the high Atacama, with correlations and causal mechanisms just being revealed. The lack of synchrony between some Atacama, northern Altiplano, and southern Altiplano events suggests different kinds or degrees of forcing mechanisms at Lake Titicaca and the southern Altiplano. This does not obscure the fact that the physical environment changed rapidly during the Quaternary, and that the plant formations and associations responded by complex alterations in their range and composition.

Table 7.4. Composition, numerical representation, and elevational range (m) in Bolivia of the nearest living equivalents of the Pislepampa palynoflora. Percentages are based on counts of 200 of all palynomorphs (% all) and of palynomorphs excluding spores of ferns and related groups (% exc.). A dash indicates specimens were not encountered in the count of 200.

Taxon	% all	% exc.	Elevation range in meters
Isoetes	1.5		
Lycopodium type 1	1.5		
Lycopodium type 2	0.5		
Lycopodium type 3	—		
Cnemidaria	0.5		
Cyathea type 1	51.6		to ~1500
Cyathea type 2	19.0		
Cyathea type 3	—		
Grammitis	0.5		
Hymenophyllum	0.5		
Pteris	2.5		
Trilete fern spore type 1	2.0		
Trilete fern spore type 2	—		
Danaea	2.0		
Monolete fern spore type 1	2.0		
Monolete fern spore type 2	1.0		
Monolete fern spore type 3	0.5		
Monolete fern spore type 4	0.5		
Podocarpus/Prumnopitys	4.0	37.5	1700–3400
Gramineae	2.5	24	
Palmae	—		
Ilex	1.5	10	180–4000
cf. *Oreopanax*	—		1100–3600
Cavanillesia	0.5		250–850
cf. *Pereskia*	—		350–2100
Compositae type 1	2.5	10	
Compositae type 2	2.0	6.0	
Compositae type 3	—		
Ericaceae	0.9	10	
Tetrorchidium	—	2.0	450–1900
Unknown type 1	—	0.5	
Unknown type 2	—		
Unknown type 3	—		

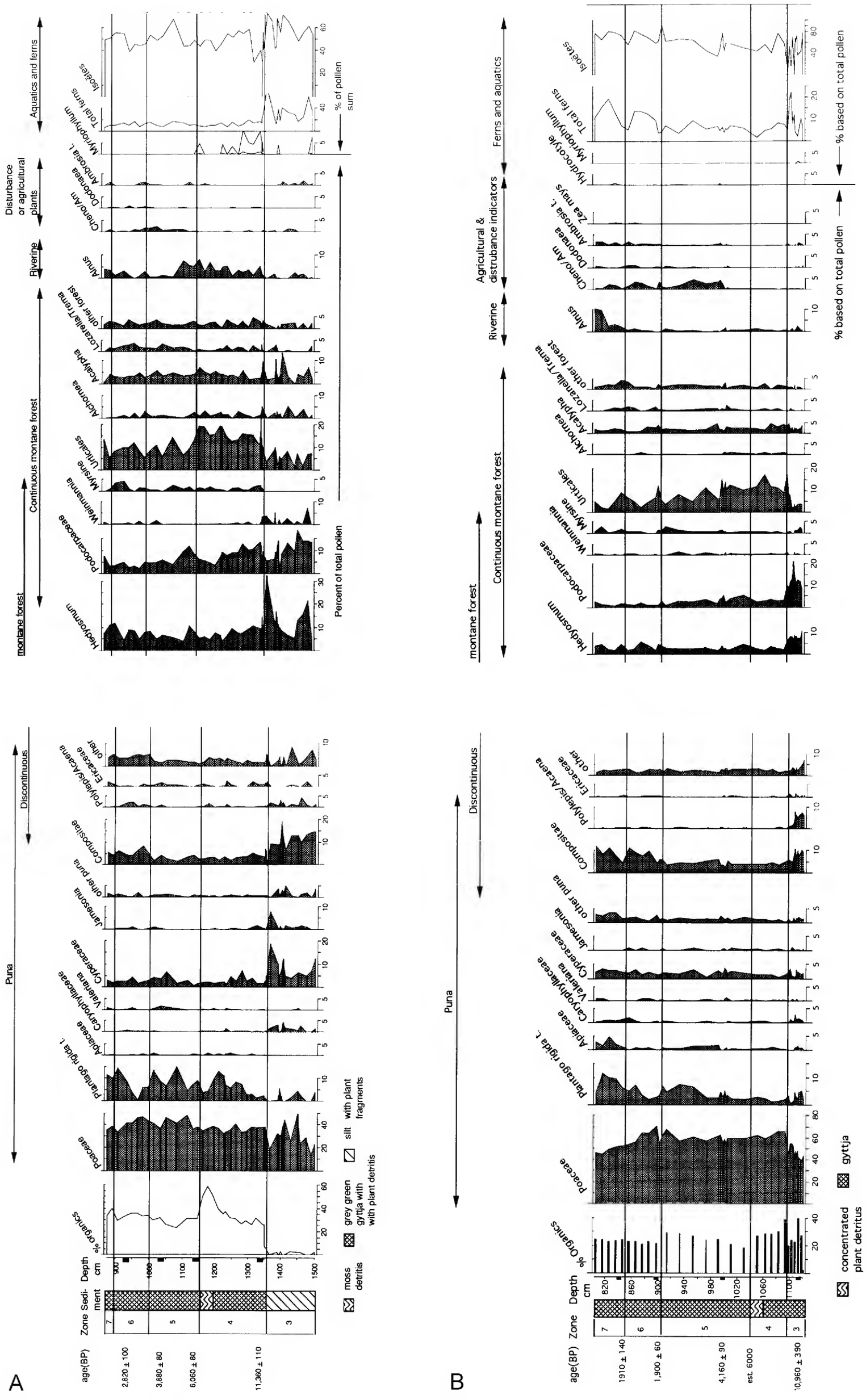


Figure 7.103. Spore and pollen percentage diagram from (A) Tuctua and (B) Jeronimo, central Peruvian Andes. Reprinted from Hansen et al. (1994), with permission of Elsevier Science Publishers, Amsterdam.

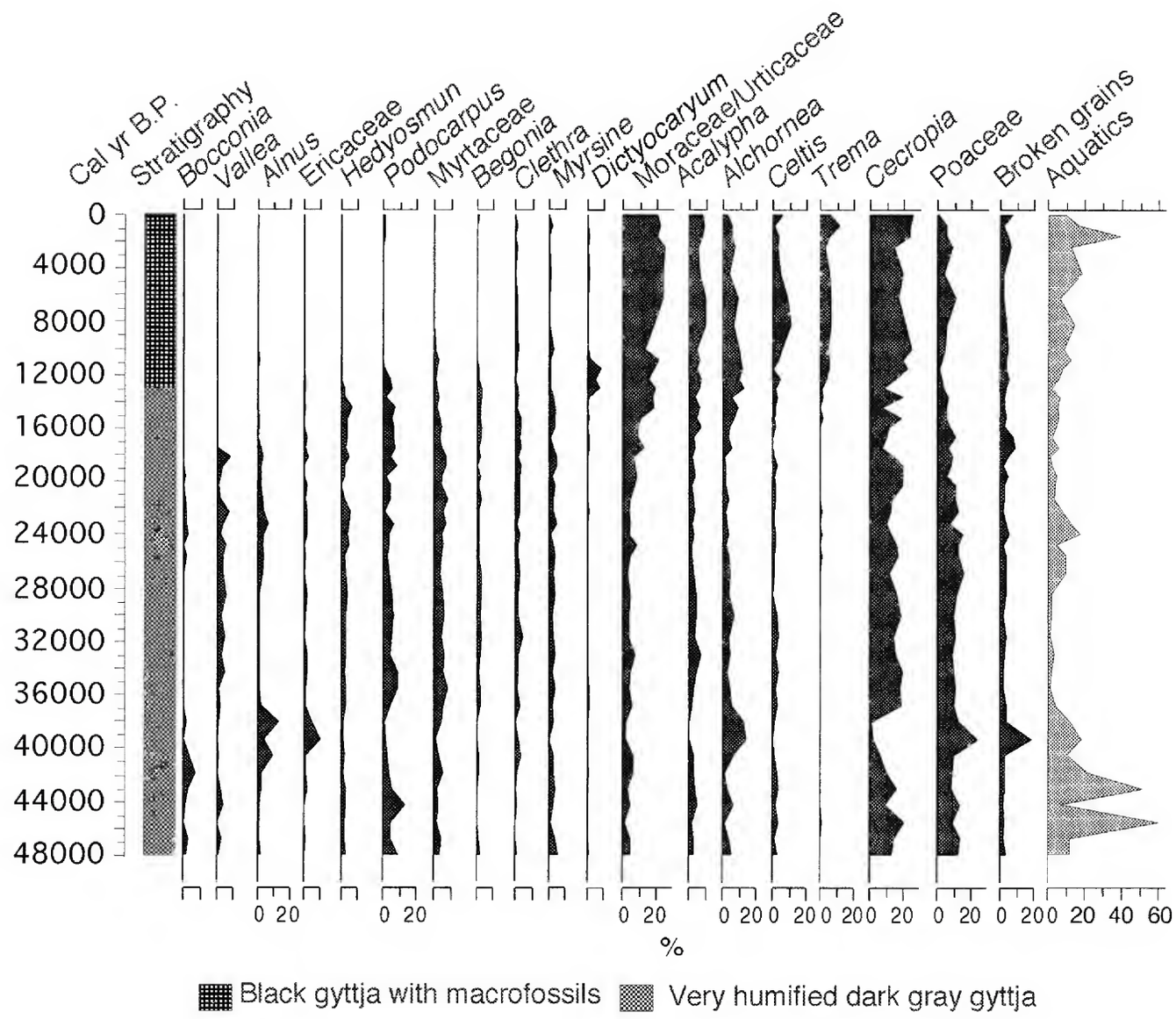


Figure 7.104. Spore and pollen percentage diagram of selected taxa, Lago Consuelo, Peru. Taxa arranged according to apparent sensitivity to warming, montane elements to left and lowland elements to right. From Bush et al. (2004). Used with permission of *Science*, American Association for the Advancement of Science, Washington, D.C.

Cold/dry or cold/wet?—For the general reader, the associations suggested between temperatures (cool or warm) and rainfall (wet or dry) may seem almost random. The proposed occurrence of wet climates during cold Late Glacial intervals in some areas (e.g., the Salar de Uyuni) is noteworthy because basic thermodynamics predicts that cold climates result in reduced evaporation from the ocean surface, less available atmospheric moisture, and globally less rainfall. In many areas, such as the tropical lowlands, this relationship often holds true. In other areas it is more complicated, as in regions with elevations ranging from sea level to over 6000 m, in places situated amid shifting climate systems (ITCZ; South Pacific and Antarctic anticyclones), and where climates are influenced by events in far-distant regions via teleconnections. Also, the Bolivian Andes Mountains are located in the transition between climatic events operating in the high northern and the high southern latitudes. The events are similar but some are asynchronous at the two poles, as expected from the Milankovitch variations but modified by overlying patterns of CO_2 concentration. The high Northern Andes of Colombia generally reflect the Northern Hemisphere pattern, the Southern Andes and adjacent regions have the Southern Hemisphere pattern, and the Central Andes are in the middle. The different temperature- and precipitation-regulating mechanisms operate on periods ranging from the 100,000-year eccentricity to D–O and Little Ice Age intervals of a few hundred years, and unless the resolution is precise and the dating accurate, a confusing picture emerges.

As will be discussed in the later section on Brazil, the generalization is that in the lowlands, cold climates often correlate with reduced precipitation. This does not necessarily mean, however, that all habitats are dry. Sites at the confluence of major river systems, localities at the base of mountains, super-wet localities at the bend of the Andes Mountains (Chapters 2, 8), edaphic characteristics (clay soils versus coarse sand), shallow basins, and areas underlain by impervious hardpan may locally perpetuate moist conditions into or during dry cycles.

In the highlands, the association between cool, warm, wet, and dry can vary among the different physiographic provinces according to the regional controls noted above. At present on the Altiplano, an easterly flow of air produces wet conditions, and a westerly flow produces dry conditions (Garreaud et al., 2003). Evidence from sediment cores in the Salar de Uyuni in the southern part of the Altiplano is interpreted, like that from Lake Titicaca, to indicate wet conditions in the Late Glacial, especially during the intervals from 50 to 38.1 Kyr B.P. and 26.1 to 14.9 Kyr B.P. (Baker et al., 2001b; Fritz et al., 2004; Chepstow-Lusty et al., 2005). The large paleolakes envisioned on the Altiplano would require an estimated 30% increase in precipitation over the present MAP. Thus, at times, the distribution of available atmospheric moisture may produce wet conditions during cold intervals in the Andean highlands, necessary for glacial growth (Thompson et al., 2005) and convenient for explaining some of the vegetation histories.

Thus, regarding these associations of temperature and moisture on vegetation history generally, it is worthwhile to distinguish between two sets of factors. One is the amount of available moisture in the atmosphere versus the regional to local distribution of that moisture. This applies particularly

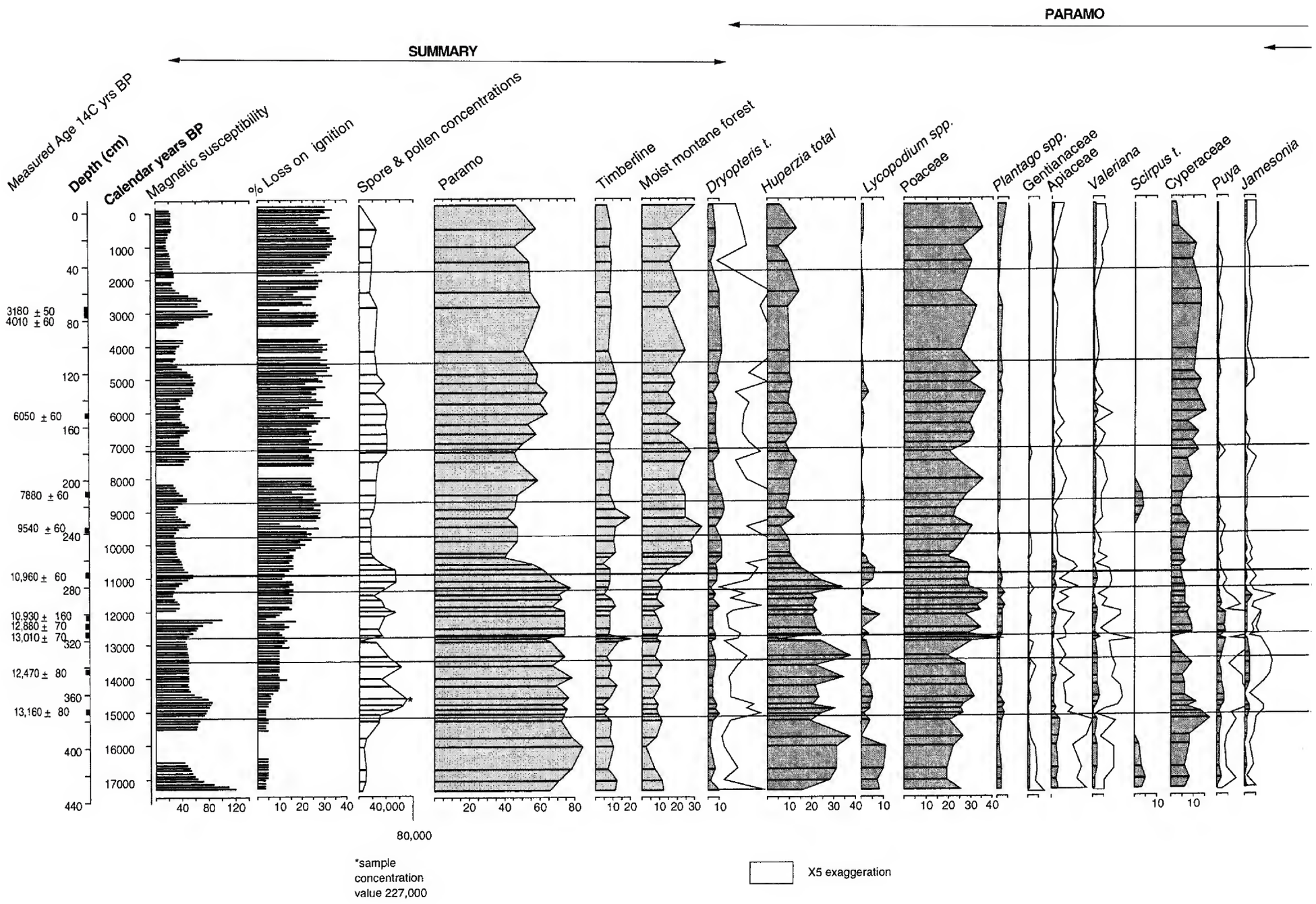


Figure 7.105. Spore and pollen percentage diagram, Laguna Chorreras, elevation 3700 m, cordillera of southwestern Ecuador. Reprinted from Hansen et al. (2003), with permission of Elsevier Science Publishers, Amsterdam. (*Continued on facing page.*)

to physiographically complex highlands in an equatorial zone where multiple climate systems converge and where there is a transition between Northern and Southern Hemisphere patterns. The other is to recognize the difference between dry or wet climate and between dry or wet habitats within that climate. As will be seen in the section on Brazil (and in Chapter 8), the distinction is important in accounting for community diversity and tracing vegetation history in the tropical lowlands.

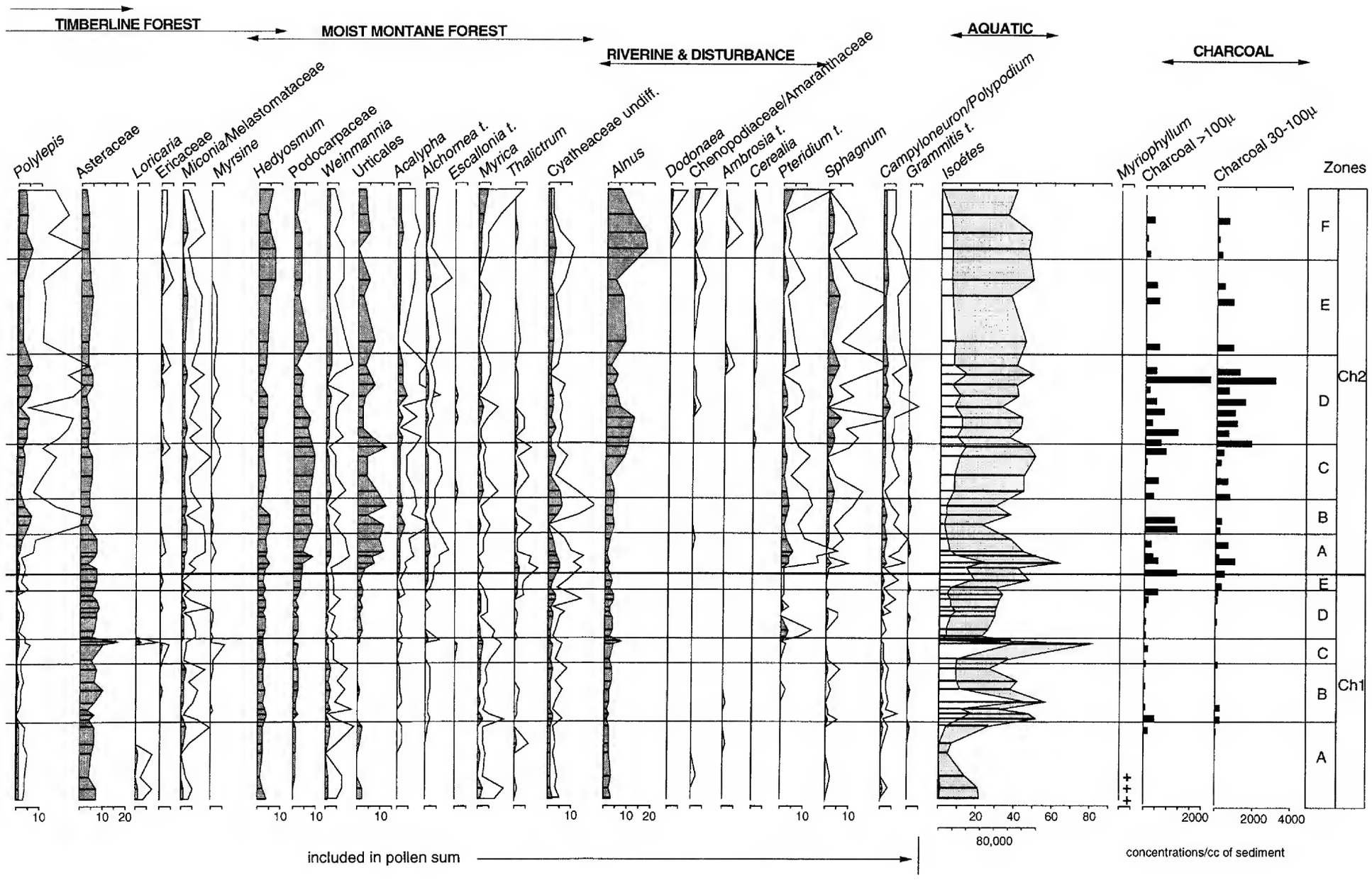
Paraguay and Uruguay

There are no Quaternary vegetational history studies for Paraguay. For Uruguay, a phytolith and pollen record indicates that the middle Holocene was dry and caused reorganization in the pre-Hispanic populations that gave rise to the early Formative societies (Iriate, 2006).

Peru

For Peru (modern pollen rain; Weng et al., 2004) and Ecuador (Mera; Chapter 8, Refugia), the paleobotanical data are meager but increasing. For example, Bush et al. (2005) in a study from Laguna de Chochos, Peru, found evidence for a warm-dry interval between 9500 and 7300 years B.P. that is important to the question of regional dryness in the Holocene (see below), and Seltzer and Rodbell (2005) note an increase in sedimentation rate at Laguna Parón ~575 ± 90 ^{14}C years B.P. coincident with the Little Ice Age.

Cores were taken at Laguna Tuctua and vicinity (11°S, 75°W) on the Junín Plain at the eastern edge of the Cordillera Oriental near 4000 m (Hansen et al., 1984, 1994; Fig. 7.103; see also Graf, 1981b). The current MAT at the site is 5°–10° C and the MAP is ~600 mm. The interpretation is that the Late Glacial was cold and dry, with no Younger Dryas interval. It warmed at the beginning of the Holocene, as suggested by an increase in pollen of the Urticales and a decrease in plants common to the high Puna such as *Polylepis–Acaena* and Asteraceae. Warming with greater moisture continued between 11,000 and 7000 years B.P. with increased Urticales and *Plantago*, and there was a mid-Holocene warm peak when cushion plants and montane forest elements declined. At 4000 years B.P., grasses and chenoams increased, indicating human disturbance. These records from the Junín Plain are consistent with the broader environmental patterns and vegetation response for the region and differ from some representing individual basins in Bolivia. A better temporal record will be forthcoming for the Junín Plain



and elsewhere with application of cosmogenic radionuclides (^{10}Be, ^{26}Al) that allow direct dating of glacial deposits older than the last glacial cycle (Smith et al., 2005a).

A core from Lago Consuelo in the lower cloud forests of the Cordillera Oriental in Peru (2000–1300 m; 13°57'S, 68°59'W) provides a perspective on the past, present, and anticipated future changes in Neotropical vegetation. At the LGM, temperatures were an estimated 5°–9° C cooler than at present in the uplands, and less cold but still substantially cooler than now in the lowlands. In the ~8000-year transition between the Ice Age and the Holocene, temperatures warmed, but at a moderate rate of ~1° C/1000 years. This compares with estimates for a current warming of 1°–4° C during the next 100 years, suggesting that although this biodiversity hot spot has undergone profound temperature changes in the past, these have never been at the unprecedented pace the communities are set to face in the near future (Bush et al., 2004).

The vegetation at Lago Consuelo during the Late Glacial cold period (Fig. 7.104) included montane elements such as *Alnus*, *Bocconia*, *Hedyosmum*, and *Vallea*. At ~21,000 years B.P., pollen of montane taxa declined, and *Acalypha*, *Alchronea*, *Celtis*, *Trema*, and Moraceae–Urticaceae increased. Warming continued until ~10,000 years B.P., when modern conditions were established. At ~9000–5000 years B.P., there was a mid-Holocene dry interval within the warming trend and montane elements migrated upslope. Interpretation of the overall vegetation is for comparatively stable and distinct Pleistocene (montane) and Holocene (lowland) communities with a long, gradual transition between them. In a complex scenario, the warming and drying are thought to have elevated the cloud base upslope, allowing wet lowland forest elements to move into the Lago Consuelo area even during a drying period. This is another variation on the complex explanations proposed for Quaternary environmental change on the Altiplano.

Human occupation, El Niños, and the Quelccaya ice cap—The earliest most certain date for humans in Peru is 12,000–11,000 years B.P. in the lowlands. Starch grains and phytoliths of *Zea mays* and *Maranta arundinacea* (arrowroot) were recovered from tools and soils around a Preceramic house at Waynuma in southern Peru (Perry et al., 2006). The date is ~4000 calibrated years B.P. and extends agriculture in the Peruvian lowlands back by 1000 years. After 11,000 years B.P., at the Pleistocene–Holocene transition, humans appear in the highlands (Aldenderfer, 1999; Rigsby et al., 2003; see also Hansen et al., 1994, p. 264). Dust records in the Quelccaya ice cap (Thompson et al., 1988) indicate two periods of high concentration at C.E. 920 and C.E. 600, each lasting ~130 years, and these are thought to correlate with intervals of pre-Incan agricultural activity. According to Sandweiss (2003; Sandweiss et al., 2001), mollusks at coastal archeological sites and cultural

records suggest that either El Niños did not affect the Peruvian lowlands between ~8000 and 5800 years B.P. or they were of lesser magnitude and frequency than at present (Haas & Dillon, 2003). The latest cycle of intense and regular El Niños started at ~5800 years B.P. and correspond to the initiation of monument temple building on the coast, while the onset of even stronger and more frequent events after 3200–2800 years B.P. corresponds to their abandonment. In contrast, flood and landslide debris near Ilo in southern Peru is interpreted as evidence for much older and intense events (Keefer et al., 1998, 2003). Two of the younger accumulations are dated at ~C.E. 1300–1400 and at ~C.E. 1607–08, and these are associated with archeological records indicating El Niño events. Similar deposits are known from 38,200 years B.P. and later (see discussion for Ecuador below), and particularly extensive ones date from the end of the Younger Dryas ~12,000 years B.P. The latter correspond with the abandonment of the Quebrada Tacahuay site (17.8°S, southernmost coastal Peru; 12,700–12,500 years B.P.). In the older records, it becomes more difficult to distinguish between deposits resulting from mega-Niños and those due to subduction and earthquake-induced landslides.

The Quelccaya ice cap (13°56'S, 70°50'W; 5670 m; MAT –3° C) includes varved deposits. These are annual layers of snow (white) and atmospheric debris (grey). The moisture to sustain the snow accumulation comes from the Atlantic Ocean across the Amazon Basin during the austral wet season (December through March), and the dust in the dry season comes from the Altiplano. During an El Niño, the moisture is reduced by >30% (Thompson et al., 1984, 1985), and in the exceptionally strong event of 1982–83, the snow at Quelccaya was blanketed with a thick layer of dust. The cores were 154.8 m and 163.6 m long, covering the past 1500 years, and within that interval varves allow climatic events to be dated with an accuracy of ~2 years. As described in Nash (2002, p. 84; see also Nash, 2007), "The Quelccaya Ice Cap was like a weather station that had been in continuous operation since A.D. 500. In its layers, archaeologists would find evidence of the El Niño floods that were said to have devastated the great coastal city of Chan Chan around A.D. 1100; they would find evidence of the decades-long drought that decimated the pre-Incan civilization of Tiwanaku at around the same time. And they would also find evidence of centuries-long El Niño– and La Niña–like periods that eerily paralleled the rise and fall of these and other pre-Incan cultures." A cold period corresponding to the Little Ice Age is evident between varves C.E. 1490 and 1880, documenting that under favorable conditions even this relatively brief pulse in cooling is detectable at equatorial latitudes.

Ecuador

Sediment cores from two highland lakes in the Cordillera Occidental of Ecuador, Laguna Chorreras (3700 m) and Laguna Pallcacocha (4060 m), reveal climate changes between 17,000 and 15,000 years B.P. and the present (Hansen et al., 2003; Fig. 7.105). In the Late Glacial (17,000–11,000 years B.P.) there was a herb páramo (*Huperzia*, *Puya*, and Asteraceae pollen assumed to be of woody species). Charcoal concentrations were low, and a climate colder and wetter than at present is inferred. In the Holocene, pollen of *Huperzia* decreases, *Puya* disappears, pollen of moist montane forest types increases, Asteraceae (possibly *Gynoxys*) is replaced by *Polylepis*, and charcoal increases, all suggesting warmer climates. In another study at Yaguarcocha, no strong evidence was inferred for a Younger Dryas event (Hansen, 1995).

The ancient history of El Niño–La Niña events is difficult to disentangle from other climatic and ocean circulation events, but studies on deposits from Ecuador are providing important information. Debris flows in Laguna Pallcacocha dating back 15,000 years indicate periods of heavy rainfall with accompanying landslides (Rodbell et al., 1999). In the younger parts of the section, these can be matched with historic records for El Niños, and occur with a frequency of 2 to 8.5 years or about equivalent to that of modern events. Flows between 15,000 and 5000 years B.P. are decidedly less intensive, the periodicity is greater than 15 years (possibly to 75 years), and apparently there were no strong El Niños between 12,000 and 5000 years B.P. Some coral evidence from Papua New Guinea also suggests waning around 8000 years B.P. A possible factor is stronger seasonal cycles induced by changes in the precession and tilt variations that disrupted the ocean circulation–temperature gradients–wind velocities necessary for initiating El Niños. The relationship between slope movement and El Niños has been quantified elsewhere in a study of landslides of the Bay Area, California, where movement increased from 27–38 mm/yr to 38–49 mm/yr (~35%) after the 1997–98 El Niño (Hilley et al., 2004). There is evidence for semi-permanent El Niño-like conditions in the Pliocene warm period (4.5–3.0 Ma; Wara et al., 2005; Fedorov et al., 2006). If increasing warmth reaches mid-Pliocene values in about 200–300 years as anticipated, semi-permanent El Niños are likely to prevail. Together with the possible increase in hurricane numbers and certainly an increase in hurricane intensity with current warming (Chapter 8), the impact on biotas and coastal habitats will be substantial. History is providing a useful insight into the conditions to come.

In the Ecuadorian lowlands, pollen, phytolith, and wood dated 33,000 to 26,000 years B.P. at San Juan Bosco and Mera are interpreted to mean a seemingly high ~7.5° C cooling below the present at 33,000–30,000 years B.P. (Bush et al., 1990). Younger sediments in northwestern Yasuní National Park in the western Amazon Basin (9500 and 2000 years B.P.) show wet and dry periods, fluctuations in water table levels, and flooding (Weng et al., 2002).

Galápagos Islands

The existing islands arose above the Galápagos hot spot 3–4 Ma (Hall, 1983; Hickman & Lipps, 1985), although submerged seamounts 5–9 Ma old may represent previous volcanic islands (Christie et al., 1992). The lava substrate and dry climate have precluded the accumulation of deep organic deposits, but limited paleoecological information is available, even though

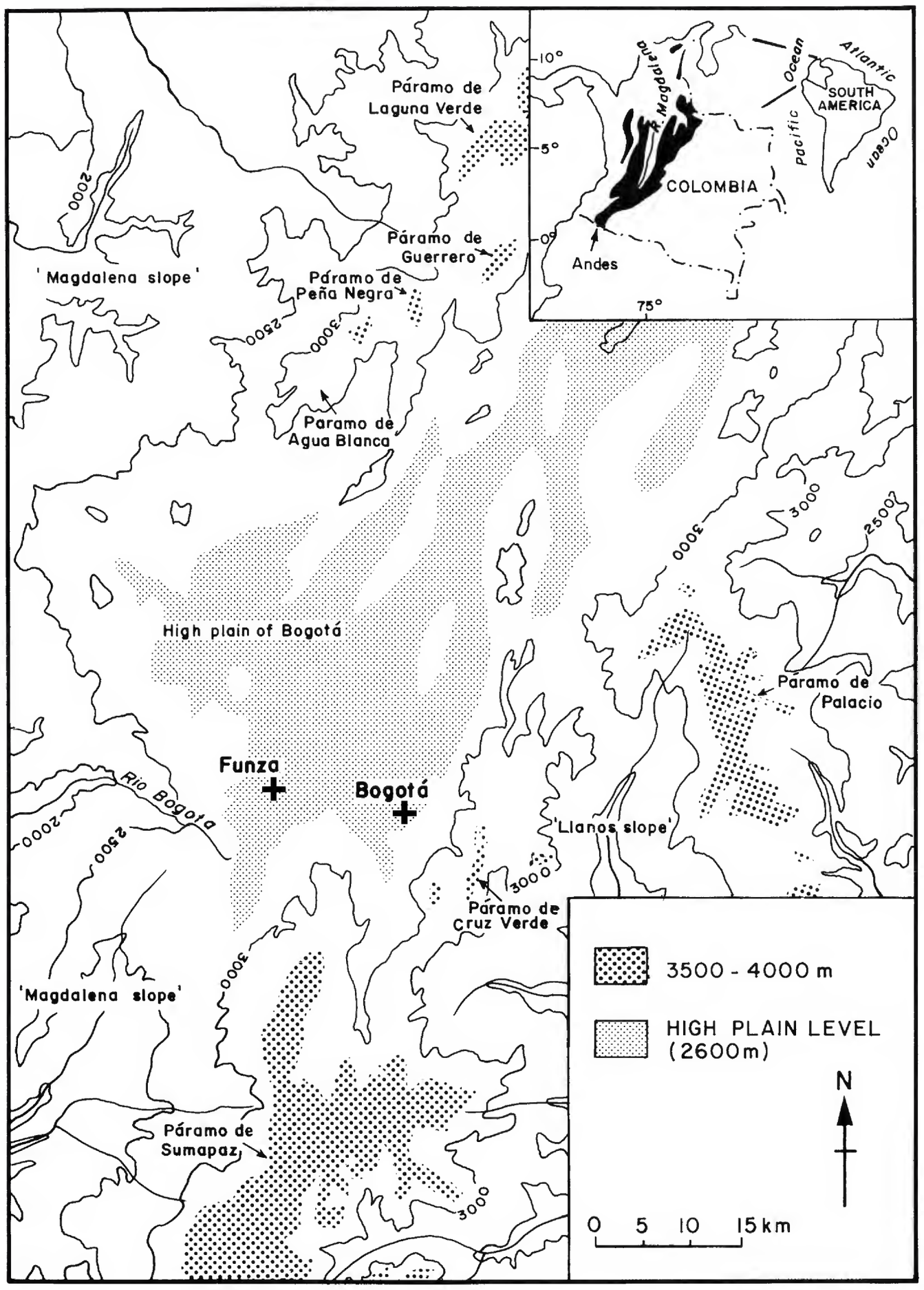


Figure 7.106. Index map of place names for the Sabana de Bogotá (High Plain of Bogotá), western side of the Cordillera Oriental, Colombia. Reprinted from Clapperton (1993), with permission of Elsevier Science Publishers, Amsterdam.

some of the early radiocarbon dates are anomalous (Colinvaux & Schofield, 1976a, b). The absence of pond sediments, or their oxidized condition, is interpreted to indicate dryness, perhaps drier than at present, for 15,000 years. Ponding began, and spores and pollen record the vegetation and environmental history from ~8600–3000 years B.P., corresponding to the mid-Holocene warm period (the older xerothermic period, or hypsithermal interval in North America). At the beginning of this interval, it became slightly more moist on the Galápagos Islands, modern conditions were then established, and only subtle fluctuations are evident for the past ~9000 years. From the Cocos Ridge just north of the Galápagos Islands (2°16'N), planktonic Mg/Ca and oxygen isotope records reveal a lowering of sea level by ~120 m at the LGM (Lea et al., 2002). This expanded the area of the islands, but probably had little effect on the kinds of plant formations present.

In an innovative approach that provides another example of the benefits of integrating history with studies on the modern biota, Beheregaray et al. (2003) detect a role for ancient volcanism in the speciation of the giant Galápagos tortoise. Isla Isabela has five taxa of the tortoise on each of its volcanoes. In an mtDNA survey, one of these (*Geochelone nigra vandenburghi*) on Volcán Alcedo was found to have three to five times less matrilineal diversity than the others. This volcano is about the same age as the others (~500,000 years), but it is the most recent to erupt (~100,000 years ago), likely causing a significant decrease in the biota. The hypothesis is that the present, genetically less-diverse population is derived from the lineage

Figure 7.107. View of the Sabana de Bogotá (High Plain of Bogotá), Colombia. Photograph courtesy of Henry Hooghiemstra.

that survived this eruption. According to Beheregaray et al. (2003), the results "emphasize the value of modern molecular population approaches in obtaining historical demographic information that cannot be discerned based on contemporary scenarios." This is complementary to another generalization emerging from the present survey; namely, that evolutionary biologists and population geneticists need no longer contend with the myth of long-term environmental or community stability in developing biodiversity models for the Neotropics. The dynamic nature of the physical landscape, climate, and the composition and range of the plant formations and habitats has been demonstrated for virtually every place surveyed and, when the resolution allows, for every major segment of geologic time, including millennial and submillennial variations.

Colombia

More than a half century of multidisciplinary and multinational research by Thomas van der Hammen and his colleagues in Amsterdam and Colombia generated a vast amount of information on the Quaternary environmental and vegetation history of Colombia. The information contributed to a fuller understanding of the paleoclimates, glacial events, vegetation history, and archeology of the High Plain of Bogotá, and it is proving to have broader relevancy. The sites are far south of the latitudes where Younger Dryas, Little Ice Age, Heinrich events, and D–O oscillations were originally described and are north of localities in central and southern South America where these events are now being recognized. The early results from Colombia played a significant role in the rethinking of climate stability in equatorial latitudes based on the CLIMAP data. Particularly important for Neotropical vegetation history and the formulation of models explaining Neotropical biodiversity and speciation was the suggestion that temperature changes and snow line depressions in the Northern Andes were too great not to have extended into and affected the biota of the Amazon lowlands.

These contributions are now continuing through the studies of Henry Hooghiemstra and his associates (Hooghiemstra, 1995; Hooghiemstra & van der Hammen, 1995; Hooghiemstra et al., 1994; see also Additional References). A focus of the investigations is the 357-m-long Funza-1 core representing the past 1.4 Ma (Hooghiemstra, 1984, 1989; Andriessen et al., 1993), and the 58-m-long Funza-2 core representing the past 3.2 Ma (Andriessen et al., 1993; Torres et al., 2005). The locality is near the village of Funza in the Basin of Bogotá (2550 m; Figs. 7.106–7.108) in the Eastern Cordillera of Colombia (4°50'N, 75°12'W). The basin has gradually subsided since the end of the Pliocene, and, except for intervals between 530 and

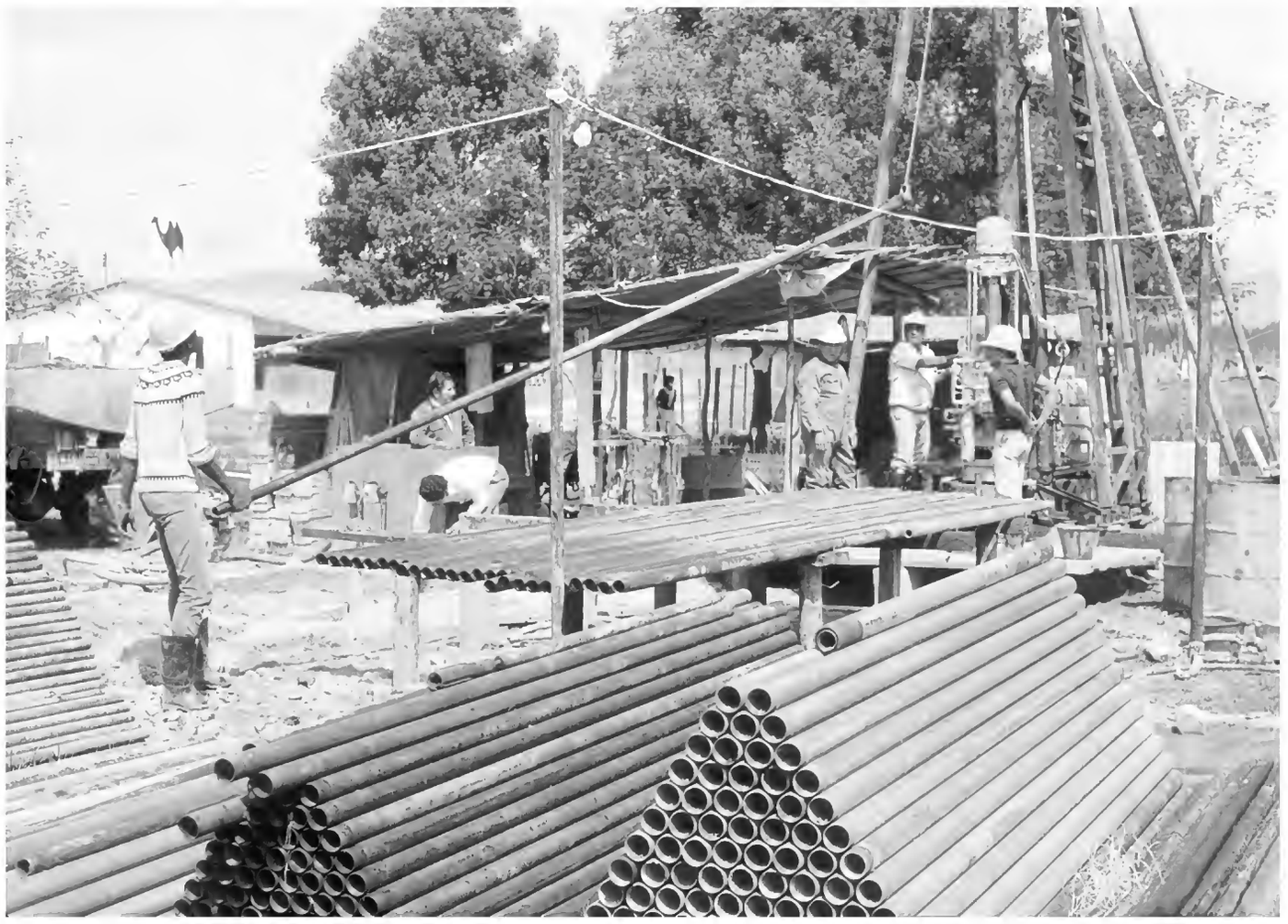


Figure 7.108. Coring operations on the Sabana de Bogotá (High Plain of Bogotá), Colombia. Photograph courtesy of Henry Hooghiemstra.

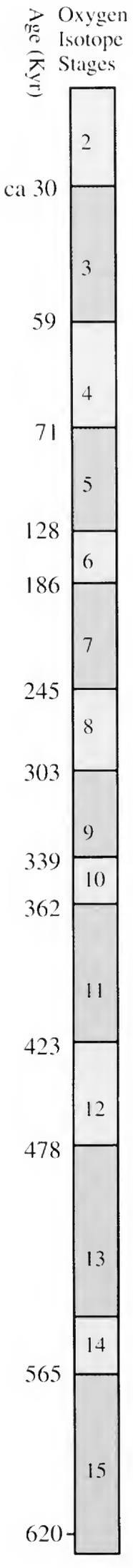


Figure 7.109. Numbered sequence and age of oxygen isotope stages. From Hooghiemstra and van't Veer (1999). Used with permission of the Past Global Changes (PAGES) Project.

325 m, this allowed accumulation of an essentially continuous sequence of lacustrine sediments (Torres et al., 2005). The lake drained ~28 Kyr B.P., and the former lake bottom is the present surface of the High Plain of Bogotá. Mountains rise to 3200 m in the immediate vicinity and to 3800 m within 40 km. The vegetation is distributed along steep altitudinal gradients so that changes in temperature, rainfall, and atmospheric CO_2 concentration cause marked alterations that are preserved in the spore and pollen assemblages. The current zones and their approximate altitudinal range are: lowland Neotropical rain forest (0–1000 m), subandean forest (warm, mixed and evergreen, lower montane forest; 1000–2300 m), Andean forest (cool, mixed and evergreen, upper montane forest; 2300–3200 m), subpáramo (>3200 m; 9.5° C isotherm), grass páramo (3500–4200 m), superpáramo (4200–4800 m), and permanent snow above ~4800 m. The principal spore and pollen types indicative of each zone are given in Table 7.5. During warm intervals, the mountain slopes were covered by forests with the upper forest limit at ~3500 m, while during cold periods various types of páramo were present, with the upper forest limit lowered to ~2000 m. In addition to the pollen assemblages, the shift to abundant grasses indicating páramo has been detected by C_3/C_4 isotopes from paleosols (e.g., kaolinite) in the Bogotá Basin (Boom et al., 2001, 2002; Mora & Pratt, 2001, 2002). The paleotemperature implied for each shift in vegetation is calculated by using a lapse rate of 6° C/km. For example, the basin presently lies in the Andean forest belt, but in glacial times the vegetation around the paleolake was subpáramo and grass páramo for a difference of 1.1 km and a calculated minimum paleotemperature ~6° C colder than at present. The tempera-

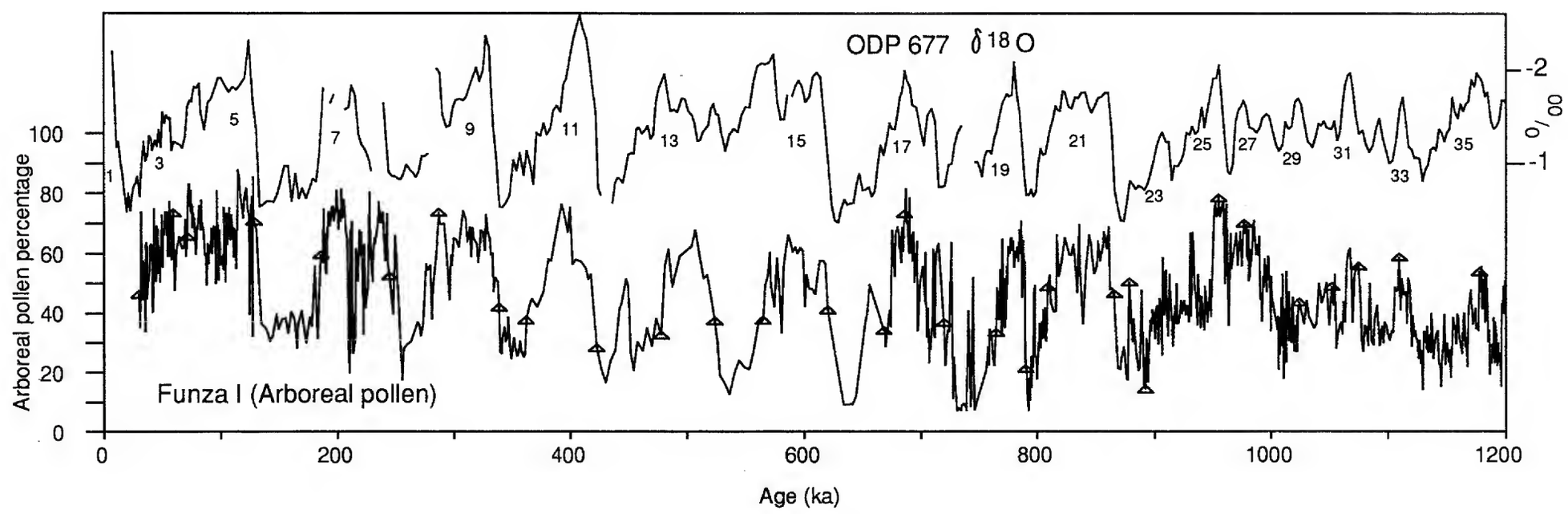


Figure 7.110. Correlation of arboreal pollen percentages from Funza-1 with Milankovitch cycles and oxygen isotope values at ODP Site 677 (Pacific Ocean). Diagram provided by Henry Hooghiemstra (pers. comm., 2006).

ture depression throughout the higher elevations of the Eastern Cordillera (2550 m) is calculated at ~8° C, extrapolating to ~5.5°–6° C cooler in the lowlands. Just to the north in the Sierra Nevada de Mérida, glaciers presently occupy ~3 km^2, while at the LGM their extent is estimated at 197 km^2.

The chronology of vegetation changes on the High Plain was established by using volcanic ash layers (tephrachronology), comparison of the Funza-1 core with dated sections of the Funza-2 core, fission-track dating (for a discussion of fission-track dating see Lamb, 2004, pp. 108–113), and initially by correlation with marine or oxygen isotope stages (MIS, OIS) at ODP Site 677 in the eastern equatorial Pacific Ocean (Figs. 7.109–7.111). These were originally set up by Emiliani (1955), and MIS 5e is noteworthy because it is the interglacial stage prior to the present Holocene. It is commonly considered as warm or warmer than the present, and it dates from ~130,000–116,000 years B.P. (Kukla et al., 2002; Shackleton et al., 2002). The last glaciation began at MIS 5d.

The marine and the terrestrial records of climate are a close match. Where differences exist between such records, the possible reasons include the different buffering (ocean)–reflectivity (terrestrial) factors operating in the two systems; different lag time response between the systems to temperature change, and between the marine versus terrestrial organisms used to monitor these differences; different sensitivities to cold intervals among the indicator organisms; or tectonic-induced changes in elevation, fluctuations in atmospheric CO_2, and precipitation/humidity/cloud-cover effects in the terrestrial realm, versus the effects of changes in ocean circulation and salinity in the marine realm during the 3.2 Ma of the Funza cores. Another reason for differences is that there may be gaps in the section, a possibility raised by the lake bed having been dry for the past 30,000 years, but these are now better defined through studies on the sedimentology by Torres et al. (2005). The temporal relationship between the terrestrial and marine records is continually being adjusted, and a summary record for Funza-1 is shown in Fig. 7.111.

A complication in reading the environmental conditions from the spore and pollen assemblages (Figs. 7.112–7.121) is that in the early part of the section (158–131 m, 735,000–569,000 years B.P.) exact modern community analogs are not present. This is because *Quercus*, an important component of the subandean and Andean forests, had not yet crossed the Panama land bridge into South America. The record of its introduction based on pollen sequences is as follows: initial scattered occurrences at 478,000 years B.P. (102 m), continuous presence at 423,000 years B.P. (92 m), and oak forests at 330,000 years B.P. (32 m). The association of *Quercus* with *Weinmannia*, as in the modern upper Andean forest, developed between 330,000 and 135,000 years B.P. and replaced *Podocarpus* as a member of that community. This means that *Quercus*, originally part of a warm forest belt, for the past 135,000 years has been part of a cold forest belt (Hooghiemstra & van't Veer,

Table 7.5. Quaternary fossil spores and pollen from the High Plain of Bogotá (Funza cores) arranged by vegetation type (from van't Veer et al., 1995). * = represented by >2%.

Subandean
Acalypha, *Alchornea*, *Cecropia*, *Clusia*

Andean
**Podocarpus*, **Alnus*, *Bocconia*, *Daphnopsis*, *Dodonaea*, *Drimys*, *Eugenia*, *Gaiadendron*, **Hydyosmum*, *Ilex*, *Juglans*, Melastomataceae, **Miconia*, **Myrica*, Myrtaceae, *Pilea*, **Quercus*, **Myrsine* (= *Rapanea*), *Styloceras*, *Symplocos*, Urticaceae, **Vallea*, **Weinmannia*; Cyatheaceae, *Borreria*, *Clethra*, *Croton bogotense*, *Monnina*, Proteaceae, *Relbunium*, *Sapium*, *Thalictrum*, *Viburnum*

Subpáramo
*Compositae, Ericaceae, **Hypericum*, **Polylepis–Acaena*

Páramo
Gramineae, *Loricaria*; *Lycopodium* foveolate-type, *Aragoa*, Caryophyllaceae, *Gentiana*, *Geranium*, **Jamesonia*, *Plantago*, Ranunculaceae, *Valeriana*

Aquatic and marsh
Isoetes, *Azolla*, Cyperaceae, *Hydrocotyle*, *Ludwigia*, *Myriophyllum*, *Polygonum*

Widespread
Artemisia, Chenopodiaceae, Rosaceae, *Rumex*, Solonaceae, Umbelliferae

Algae
Botryococcus, *Coelastrum*, *Pediastrum*

Other ferns and allied groups
Lycopodium reticulate-type, *Selaginella*, *Hymenophyllum*, *Hypolepis*, *Lophosoria*, monolete spores, *Ophioglossum*

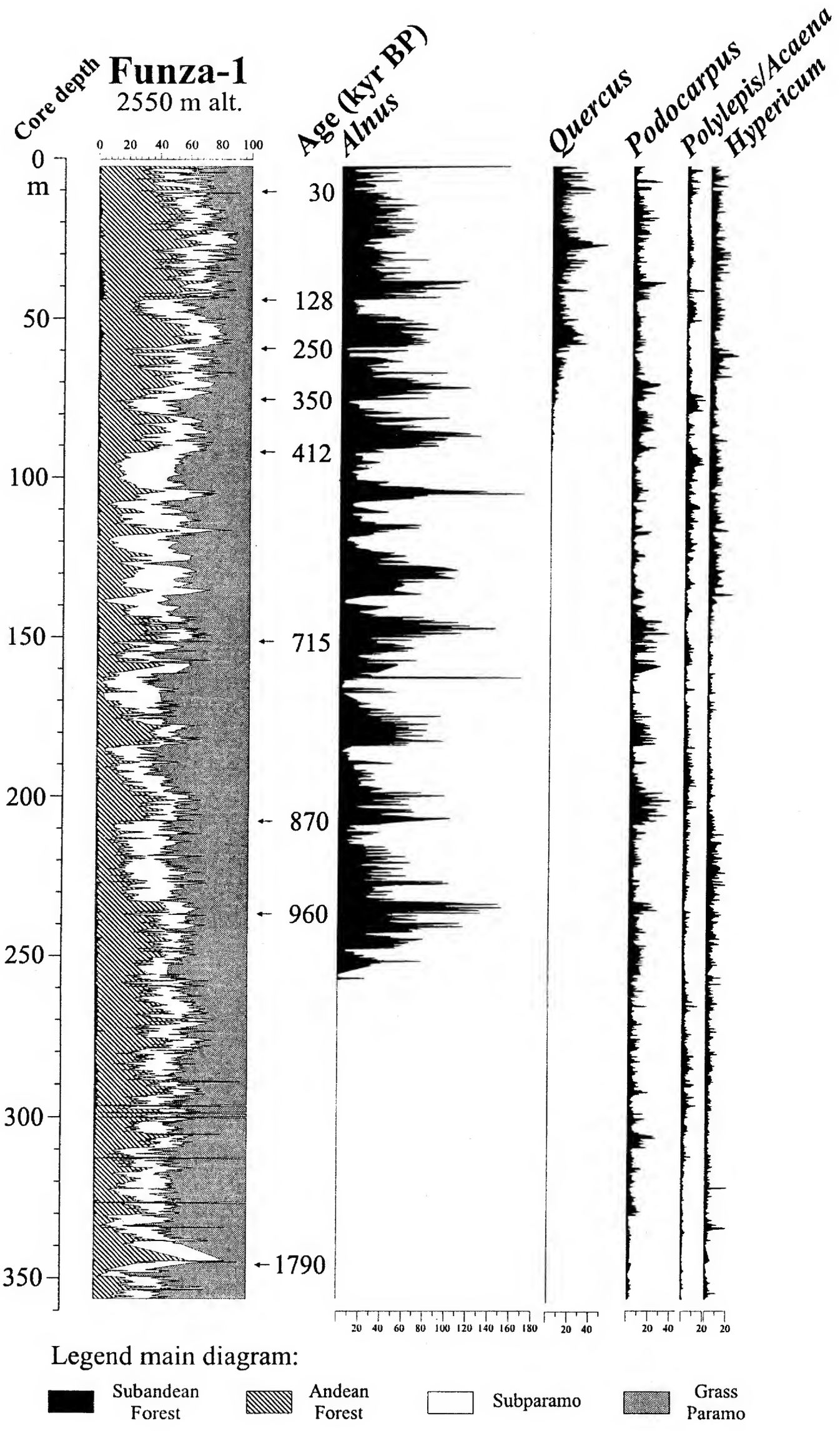


Figure 7.111. Pollen diagram from Funza-1 showing forest-páramo change from 1.8 Ma to 30 Kyr. Records for the trees *Podocarpus*, *Alnus*, *Quercus*, and *Polylepis* and the shrub *Hypericum* are shown separately. Figure provided by Henry Hooghiemstra.

1999; van't Veer & Hooghiemstra, 2000). This may indicate some adaptation of the *Quercus* lineage to colder conditions, that one species of oak replaced another, and/or that the genus was expanding into a fuller range of its ecological potential. *Alnus* was introduced into northern South America earlier at ~1 Ma.

At the opening of the sequence from 3.2 to 2.7 Ma, conditions were moderately warm, then turned colder between 2.7 and 2.2 Ma, by 4°–5° C, corresponding to global cooling revealed by expanded Arctic glaciation. The oscillations after that time are shown in Fig. 7.111. An aspect of the climate revealed by the long interval of the Funza-1 core is that for the last ~800,000 years the principal temperature change and the primary movement of the forest belts followed a periodicity of 87,000–100,000 years, and that is close to the eccentricity cycle of ~100,000 years. A secondary precession period of ~23,000 years is present throughout (Hooghiemstra et al., 1993; Fig. 7.110). Orbital forcing of shorter cycles is evident in pollen assemblages from several parts of Latin America. Recall that the precession cycle is suggested by the Salar de Uyuni assemblages from the Altiplano. However, examples of the longer eccentricity cycle are rare for terrestrial environments in the Neotropics because long and essentially continuous sections are required.

Another study made possible by the considerable age of the Funza-2 core was to model the individual roles of temperature, precipitation, and atmospheric CO_2 (through a range of 170–340 ppmv) in determining the climates, and to test which combination of factors was likely to produce changes in the plant formations similar to those observed along the core (Marchant et al., 2002). CO_2 patterns were based on the Vostok (Antarctica) ice core data, and a BIOME-3 vegetation model was run under different environmental parameters to simulate changes in vegetation. The spore and pollen assemblages showed that in glacial times the grass–shrubland páramo formation was dominant, while in the warmer interglacials the mixed forest was dominant. The two became co-dominant at ~170 Kyr (viz., both present near the sedimentary basin), and they later became out-of-phase (cold-warm fluctuations) and then co-dominant again at 120 Kyr until the LGM. The out-of-phase period was an interval of changeable but generally low CO_2 concentration, and within the average CO_2 values along the core, a modeled change of ~5.5° C is required to lower the páramo to the level of the lake basin. The ground-truth value from Funza-2 based on modern analogs is 5°–9.5° C, and the overall value for the High Plain of Bogotá is 8° C at >2600 m and 2.5°–6° C at sea level (Wille et al., 2000). In a later study (Marchant et al., 2004), the authors further conclude that "at lower altitudes it is apparent that moisture is the dominant control on driving vegetation change [Chapter 8] whereas temperature becomes more important at higher altitudes."

The climates and vegetation for the Late Glacial and Holocene have been reconstructed on the basis of palynology, glacial geomorphology, and other evidence for the Eastern Cordillera between latitudes ~7°–3°N; the Central Cordillera ~200 km to the west (Parque Nacional Natural Los Nevados, Melief, 1985; Massif Ruíz-Tolima, Thouret et al., 1996), where volcanism played an important role in the history of the vegetation; and the Sierra Nevada de Santa Marta 500–600 km to the north (Kuhry et al., 1993). El Abra (Schreve-Brinkman, 1978) is located within the Eastern Cordillera on the High Plain of Bogotá, and Fúquene (van Geel & van der Hammen, 1973) is in the neighboring Ubaté-Chichinguirá Basin. Summaries of these and other localities are provided by Kuhry (1988), Wille et al. (2001), and González-Michaels et al. (2002). The sequence is given below (stadials are periods of glacial standstill or advance, cold or cooling; interstadials are periods of glacial retreat, warm or warming; temperature values presented are relative to modern temperatures):

Early and Late Fúquene stadials, 22.5–19.5 and 17.0–14 Kyr, ~–7°–8° C, dry, upper forest line ~2000 m (Hooghiemstra & van der Hammen, 1993), forests limited in the vicinity, principal tree *Quercus*, with a La Laguna interstadial between 19,500 and 17,000 years B.P. when temperatures rose ~4° C (Helmens et al., 1996);

Susacá interstadial, 14–13 Kyr, –4° C, dry, upper forest line 2500 m;

La Ciénega stadial, 13–12.4 Kyr, –6° C, dry, upper forest line 2200 m;

Guantiva interstadial, 12.4–10.8 Kyr, temperatures rising to only 1°–2° C below present (interval interpreted as not represented at Lake Titicaca), wet, upper forest line 3100 m (pioneer *Dodonaea*, *Rapanea* replaced by *Alnus*, *Quercus*);

El Abra stadial (= Younger Dryas), 10.8–9.5 Kyr, –3°–4° C (interval interpreted as not represented at Lake Titicaca in Bolivia, Junín Plain in Peru, or Yaguarcocha in Ecuador; interpreted as present at Salar de Uyuni in Bolivia), dry, upper forest line 2700 m (*Alnus* replaced by *Myrica*, Asteraceae scrub, and open grassland);

Holocene (9.5–7.0 Kyr), warm (–1°–0° C) and ± dry, upper forest line 3100 m;

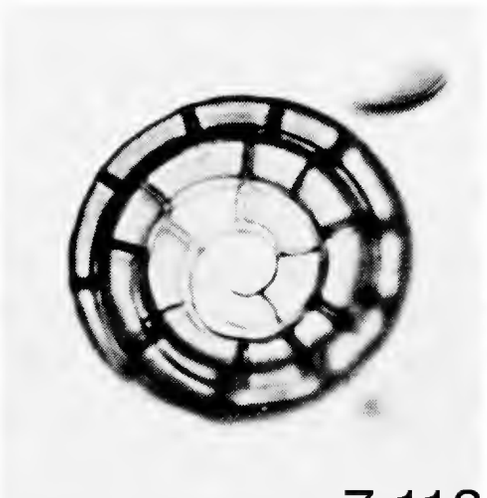
Holocene (7–1.8 Kyr), warm (+1°–0° C), wet, upper forest line 3500 m (*Alnus*, mixed *Cecropia–Quercus* forest; *Zea* present from ~6.6 Kyr onward, little early impact on the vegetation), later in interval (5.0–1.8 Kyr) *Cecropia* disappears from *Quercus* forests, then *Weinmannia* with *Hedyosmum* replaces *Quercus* in some areas; and

Holocene (1.8 Kyr–present), warm (±0° C) ± wet, upper forest line 3300 m.

Regarding the inconsistency of evidence for the Younger Dryas in northern South America (van der Hammen & Hooghiemstra, 1995), van't Veer et al. (2000) note that the associated drought likely eroded sediments in hydrologically sensitive areas. If so, the event will be evident only from adjacent sites with well-dated sections continuous between ~11,000 and 9000 years B.P.

The earliest presence of humans on the High Plain of Bogotá is difficult to establish because artifacts in the oldest strata may not be in situ. They consist of sporadic chert flakes and

7.112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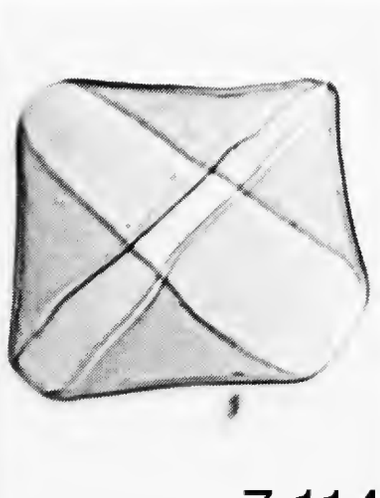
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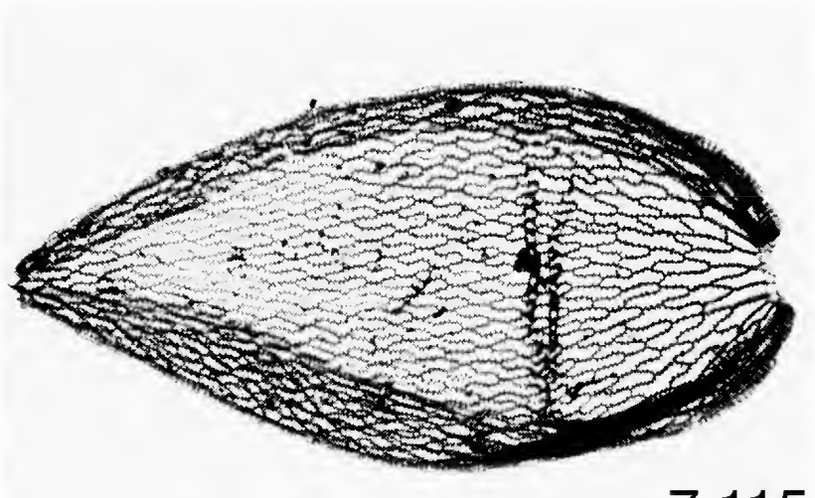
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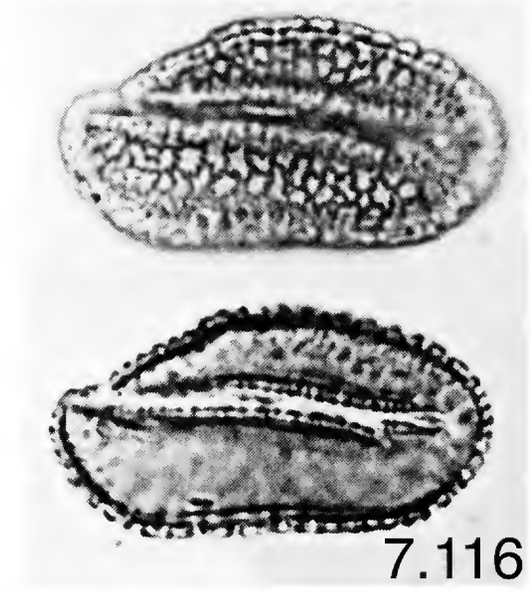
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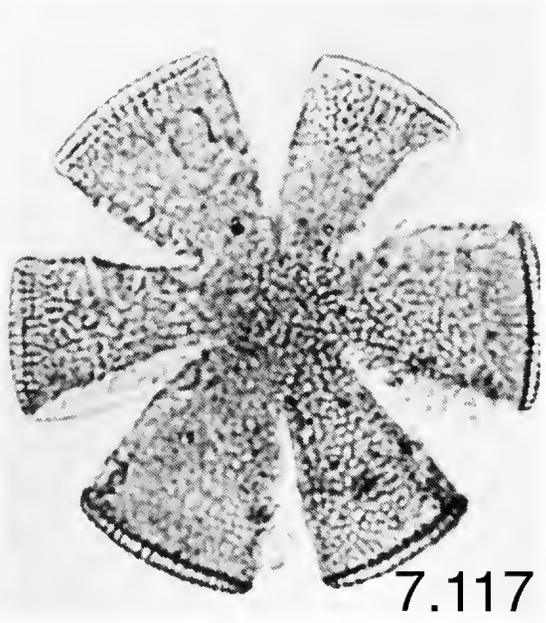
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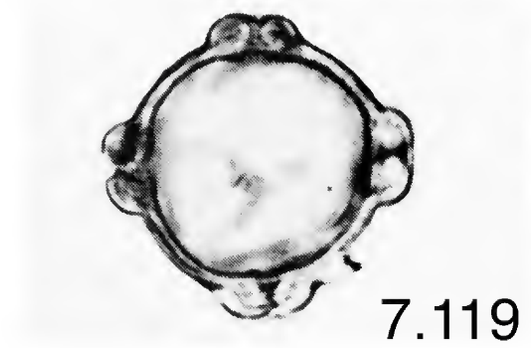
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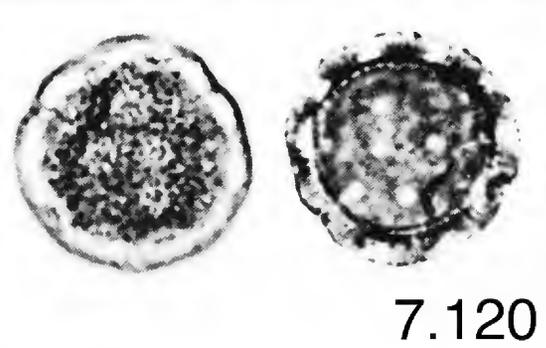
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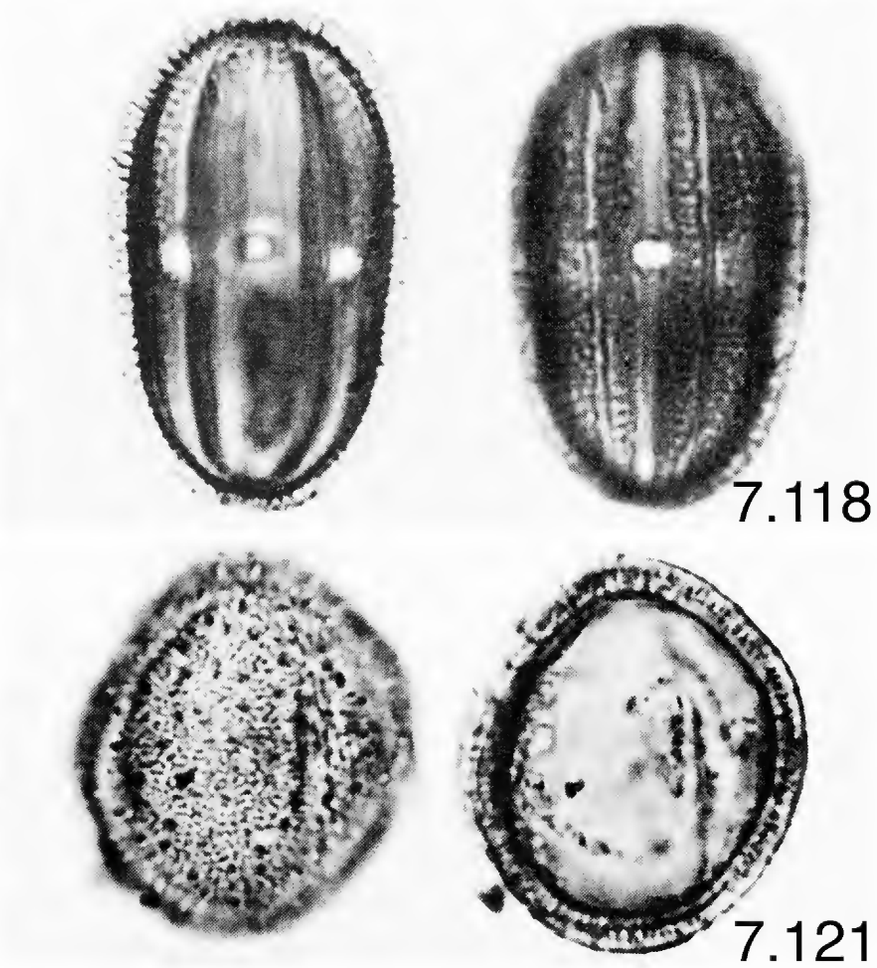

7.121

Figures 7.112–7.121. Spores and pollen from the Quaternary of Colombia. 7.112. *Pleospora* (fungal spore). 7.113. *Helicoon pluriseptatum* (fungal spore). 7.114. *Mougeotia laetevirens* (algal zygospore, Zygnemataceae). 7.115. *Sphagnum subsecundum* (Bryophyta, Musci). 7.116. *Puya* (Bromeliaceae). 7.117. *Merremia* (Convolvulaceae). 7.118. *Dicliptera* (Acanthaceae). 7.119. *Myriophyllum* (Halorag(id)aceae). 7.120. Caryophyllaceae. 7.121. *Valeriana* (Valerianaceae). Figs. 7.113, 7.115 from Kuhry (1988), used with permission of J. Cramer-Gebrüder-Borntraeger Verlag, http://www.borntraeger-cramer.de. Remaining figures from Hooghiemstra (1984), used with permission of Koeltz Scientific Books, Koenigstein, Germany.

scrapers and come from levels in the El Abra rock shelters (Hurt et al., 1976) dated at 12,500 years B.P. (Guantiva interstadial; ~modern temperatures, moist, forested). Between 10 and 9 Kyr (El Abra stadial), the number of artifacts increases from 31 to 331 (the principal activity was hunting the deer, *Odocoileus*), early cultivation is evident ~6.6 Kyr, and agriculture with a ceramic complex begins ~2.5 Kyr (van der Hammen & Correal Urrego, 1978; Gómez et al., 2007). It was probably only near the latter date and afterward that the vegetation was affected by humans to an extent that would be apparent in spore and pollen diagrams.

Cores from the Panama Basin, offshore from the Northwestern Andes at considerable depths of 3473 and 2200 m, show a sequence interpreted as cold and humid (39,410–28,120 years B.P.), coldest and driest at the Last Glacial Maximum (28,120–14,500 years B.P.), a transition period (14,500–11,200 years B.P.), a humid period (11,300–5600 years B.P.) with an intervening mid-Holocene dry interval, and present conditions with evidence of human disturbance (after 5600 years B.P.; González et al., 2006). In contrast, from onshore sediments Vélez et al. (2006) interpret the mid-Holocene as humid on the Pacific coast of northwestern Colombia, with increased cycles of precipitation related to La Niña phases.

Assemblages from cores at Laguna Loma Linda, east of Bogotá in eastern Colombia at an elevation of 310 m (Behling & Hooghiemstra, 2000), Laguna Las Margaritas (altitude 290 m; Wille et al., 2003), El Pinal (Marchant et al., 2006), and other sites in the lowlands (e.g., Laguna Piusbi; Behling & Hooghiemstra, 1998a, 1999) give an indication of the vegetation for the past ~11 Kyr at the transition between the savannas of Los Llanos Orientales and the lowland Neotropical rain forest, and in the Chocó. At Laguna Loma Linda between 8700 and 6000 years B.P., the vegetation was grass savanna, with *Byrsonima* and *Curatella* as the savanna trees, and a poorly developed gallery

forest (rainfall lower than at present and distinctly seasonal). In general, it was during the early and middle Holocene (11,000–6000 years B.P.) that the region's tropical dry forest reached its (most recent) maximum Quaternary expanse (Marchant et al., 2006). This is the interval between 9500 and 7000 years B.P. described from the High Plain that was also warmer and drier than at present. At 6000–3600 years B.P., rainfall increased, gallery forest developed, and the lowland Neotropical rain forest moved into the area (pollen of *Acalypha*, *Alchornea*, *Cecropia* abundant, Moraceae–Urticaceae, Myrtaceae, *Myrsine* increases; Poaceae decreases). This is the interval between 7000 and 1800 years B.P. on the High Plain that was warm and wet. The expectation based on regional trends would be that lowland rain forest continued to expand, but at 2300 years B.P., grass savanna with *Mauritia* palms became dominant due to human impact that continues to the present. At Laguna Las Margaritas the early period of dry grass savanna is extended back to 11,150 years B.P. with subsequent shifts between savanna and forest. Between 2500 and 1000 years B.P., abundant pollen of *Mauritia* indicates local areas of standing water (also in the Carimagua area; Berrío et al., 2000), and expansion of savanna during this time corresponds to human disturbance. At Laguna Piusbi in the Chocó, the vegetation has been moist forest for the past 6000 years (Behling & Hooghiemstra, 1998b).

Origin of Neotropical savannas—For savannas to develop in tropical environments prior to human presence, there must be a coincidence of several factors. One is edaphic conditions that create a nutrient and water deficit limiting the growth of trees, and this is often provided by soils derived from erosion of ancient sandstone substrata. In tropical habitats, the potential water deficit is usually overridden by high rainfall and/or high water tables, so another component favoring savanna development is a climatic change toward dry or more distinctly seasonal rainfall. It has been suggested that human impact via fire, overgrazing, or shifting agriculture is necessary for the presence of savannas. This is certainly true for their origin, maintenance, and expansion in marginal forested areas. However, the data from Los Llanos Orientales–rain forest ecotone discussed above show that in at least some regions, abundant pollen of Poaceae, *Byrsonima*, and *Curatella*, together with few forest trees, is evident in the lowlands prior to any evidence of human presence. This suggests that the edaphic factor, present from ancient geologic times, had to be supplemented by dry climates before the development of savannas could begin. From the Late Cretaceous through the Tertiary, fluctuating water tables would not be involved because sea levels were typically high. The first time that edaphic dryness appears to have been augmented by significant periods of climatic dryness (and supplemented by low water tables) was in the late Pliocene and especially in the full glacial intervals of the Pleistocene (Behling & Hooghiemstra, 2001). This is the likely time of origin and the beginnings of widespread, sustained Neotropical savannas. The presence of modern-day Neotropical savannas during a time of greater rainfall and high water tables likely is a consequence of human impact. The same scenario is proposed for the origin and spread of grasslands but with somewhat greater edaphic and climatic dryness eliminating the savanna trees. Regarding upland palm savannas (as opposed to vereda), I know of no instances where regional paleobotanical data show high levels of palm remains associated with abundant grasses in the absence of evidence for human disturbance. Therefore, I regard upland Neotropical palm savannas of any significant extent or duration to be of anthropogenic origin.

A consideration of the Quaternary vegetation in the lowlands of Colombia leads to the history of the lowland Neotropical rain forest, and this will be deferred until Chapter 8 (Refugia) and after discussing the Quaternary rain forest of Brazil. There are records from the Caquetá River Basin in the central Colombian Amazon back to 11,150 years B.P. showing that between 11,150 and 4730 years B.P., the swamp was smaller than at present, more shallow, and with abundant *Mauritia* (Behling et al., 1999). The basin was drier, which may have been due to different drainage patterns and/or to changes in climate. Either way, the later development of rain forest, the presence of *Podocarpus* in the Late Glacial and Holocene, an increase in *Cecropia* (disturbance), then recovery (increase in *Caryocar*, *Protium*, and *Psychotria*) and alternating periods of dry (drained) and wet soils document vegetation changes in the Amazonian lowland Neotropical rain forest at sites in Colombia during the Holocene. In contrast, a core from lake deposits in the Chocó rain forest of the Pacific lowlands shows similar vegetation present for the past 6000 years (*Acalypha*, *Alchornea*, *Cecropia*, *Euterpe–Geonoma*, Fabaceae, Melastomataceae–Combretaceae, *Mimosa*, Moraceae–Urticaceae, *Piper*, *Protium*, *Sloanea*, *Socratea*, *Wettinia*; Behling & Hooghiemstra, 1998b).

Venezuela

A site providing valuable context information on Late Glacial and Holocene environments in the lowlands is the Cariaco Basin off the northern coast of Venezuela (~10°N). Sediments in the basin are laminated (light and dark) due to changes in upwelling that affect nutrient supply and the concentration of marine microorganisms. Patterns in the upwellings are caused by reorganization of the North Atlantic thermohaline circulation, and the effect is expressed as far south as the Cariaco Basin in the form of subdecade to century-long oscillations (Hughen et al., 1996). Marine microfossil and isotopic data from the basin indicate that during marine isotope stage 11 (423–362 Kyr B.P.) sea levels were 10–20 m higher than today due to a reduction of the West Antarctic and Greenland ice sheets (Poore & Dowsett, 2001). This undoubtedly would have inundated much of the coastal and low-lying areas, with the effects extending inland along estuaries. Titanium concentrations in the basin sediments give other indications of the climate (Haug et al., 2001). Titanium is a terrestrial element, and its fluctuation in marine basin sediments is a reflection of the extent of outwash from sheet flooding and river flow (viz., MAP). The record from the Cariaco Basin extends back 14,000 years and, using X-ray fluorescence to identify layers, it also has

Table 7.6. Representative Quaternary plant fossils from South America. Some citations include cf. identifications. Refs. = references, as follows, Argentina/Tierra del Fuego: 1 = Matteri 1988, 2 = Heusser 1995a, 3 = Heusser 1995b, 4 = Mancini 1998, 5 = Paez et al. 1999, 6 = Prieto 2000, 7 = Quattrocchio and Borromei 1998; Chile: 8 = Grosjean et al. 2001 (part B of diagram with taxa mostly identified to "type" not included), 9 = Heusser et al. 1996a, 10 = Heusser et al. 1996b, 11 = Latorre et al. 2003 (middens), 12 = Heusser et al. 1999; Bolivia: 13 = Paduano et al. 2003; Peru: 14 = Bush et al. 2004, 15 = Hansen et al. 1994; Ecuador: 16 = Bush et al. 1990, 17 = Hansen et al. 2003; Galápagos Islands: 18 = Colinvaux and Schofield 1976a, b, 19 = Schofield and Colinvaux 1969; Colombia: 20 = Hooghiemstra 1984; Venezuela: 21 = Rull et al. 1987, 22 = Salgado-Labouriau et al. 1992, 23 = Salgado-Labouriau et al. 1988, 24 = Leyden 1985, 25 = Salgado-Labouriau 1980; Trinidad: 26 = Berry 1925e; Brazil: 27 = Duarte 1959, 28 = Behling 1996, 29 = Ledru et al. 2001, 30 = De Oliveira et al. 1999, 31 = Barberi et al. 2000, 32 = Behling 1997b, 33 = Behling et al. 2004.

Fungi	
Asterina	20
Athelia	20
Gaeumannomyces cf. *caricis*	20
Gelasinospora adjuncta	20
G. retispora type	20
Helicoon pluriseptatum	20
Hiospira	20
Micropeltis	20
Microthyrium	20
Neurospora	20
Pleospora	20
Sphaerodes	20
Spirotremesporites ecuatorialis	20
S. simplex	20
cf. *Stemphyllum*	20
Tetraploa aristata	20
Tilletia sphagni	20
Ulospora	20
Algae/Protista	
Amphitrema flavum	20
Arcella arenaria (Protista)	20
A. brasiliensis	20
A. catinus	20
A. discoides	20
A. polypora	20
Assulina seminulum	20
Botryococcus	8, 21, 22, 24, 25, 29, 33
B. braunii	20
Chlamydomonas	31
Coelastrum	25
C. reticulatum	20
Cosmarium	20
Debarya glyptosperma type	20
Hystrichosphera	20
Mougeotia	31
M. laetevirens type	20
Pediastrum	6, 13, 21, 22, 25
P. boryanum type	20, 24
P. duplex type	20, 24
P. integrum	8
P. patagonicum	8
Pseudoschizaea	31
Scenedesmus	22
Spirogyra	20
Tetraedron	22
Zygnema	20
Zygnemataceae	25, 31
Bryophyta	
Musci	
Bartramia?	20
Breutelia?	20
Bryum?	20
Dicranella?	20
Didymodon	1
Drepanocladus?	20
cf. *Leskea*	20
Meesia	20
Rhodobryum?	20
Sphagnum	2, 3, 7, 12, 17, 20, 32, 33
Weissia	20
Anthocerotae	
Anthoceros	20
Hepaticae	
Phaeoceros	20
P. laevis	32, 33
Riccia	20
Ferns and related groups	
Acrostichum (Pteridaceae)	20
Adiantum (Pteridaceae)	20
Alsophila (Cyatheaceae)	23
A. cf. *elegans*	32
Anemia (Schizaeaceae)	20, 32
Asplenium (Aspleniaceae)	20
A. serra type	20
Athyrium dombeyi type (Dryopteridaceae)	20
Azolla (Salviniaceae)	20
A. filiculoides	10, 19
A. microphylla	20
Blechnum imperiale type (Blechnaceae)	33
B. (*Salpichlaena*) *volubile*	20
Botrychium (Ophioglossaceae)	12, 20
B. dusenii	3
Campyloneurum–Polypodium (Polypodiaceae)	17
cf. *Cheilanthes* (Pteridaceae)	20, 23
Cnemidaria–Hemitelia (Cyatheaceae)	23
Crassoretitriletes vanraadshooveni (form genus–species)	20
Ctenitis (Dryopteridaceae)	20
C. pleiosoros	18
C. sloanei	18
C. subincisa type	20
Cyathea (Cyatheaceae)	13, 18, 20, 21, 23, 30, 32
Cyathea (*Alsophila–Sphaeropteris*)	20
C. (*Nephelea*) *cuspidata* type	20
C. escuquensis type	20
C. frigida type	20
C. horrida type	20
C. cf. *schanschin*	32
Cyathea (*Sphaeropteris*)	20
Cyathea (*Trichipteris*)	20
Cyatheaceae	17, 20
Cystopteris diaphana type (Dryopteridaceae)	20
Cystopteris–Hypolepis	20
Dennstaedtia (Dennstaedtiaceae)	20
Dicksonia (Dicksoniaceae)	23, 33
D. sellowiana type	20, 32
Dryopteris (Dryopteridaceae)	17
Elaphoglossum/Asplenium/Hemidictyum (Dryopteridaceae/Aspleniaceae/ Dryopteridaceae)	17, 20
E. cuspidatum	20

Table 7.6. Representative Quaternary plant fossils from South America. *(Continued)*

Eriosorus flexuosus (Pteridaceae)	20
Grammitis (Polypodiaceae)	17, 20, 23
G. (*Ctenopteris*) *moniliformis* type	20
Gymnogramma (Gymnogrammaceae) (now distributed among several genera)	32
Hemitelia (see *Cnemidaria*)	
Histiopteris incisa type (Dennstaedtiaceae)	20
Huperzia (*Lycopodium*; Lycopodiaceae)	17
H. (*Lycopodium*) *fuegiana*	12
H. (*Lycopodium*) *selago*	9
Hymenophyllaceae	12
Hymenophyllum	32
H. myriocarpum	20
H. trichophyllum type	20
Hypolepis hostilis type (Dennstaedtiaceae)	20
Isoetes (Isoetaceae)	12, 13, 15, 17, 21, 22, 23, 32, 33
I. boyacensis type	20
I. savatieri	12
Jamesonia (Pteridaceae)	15, 17, 20
Lindsaea (Dennstaedtiaceae)	23
Lophosoria (Lophosoriaceae)	23
L. quadripinnata	12, 20, 32
Lycopodium (Lycopodiaceae)	7, 13, 17, 20, 21, 23
L. alopecuroides	32
L. cernuum	18, 20, 31
L. cf. *clavatum*	18, 32
L. cuatrecasasii	20
L. curvatum type	20
L. foveolate (form species)	20, 21, 22, 23, 32
L. jussiaei type	20
L. magellanicum	2
L. passerinoides	18
L. trianae	31
Marattia cf. *verschaffeltiana* (Marattiaceae)	32
Nephrolepis (Davalliaceae, Nephrolepidaceae)	18
cf. *Onychium* (Pteridaceae)	20
Ophioglossum crotalophoroides (Ophioglossaceae)	20
O. engelmannii type	20
Osmunda (Osmundaceae)	32
Paesia viscosa (Dennstaedtiaceae)	20
Pilularia (Marsileaceae)	20
Pityrogramma (Pteridaceae)	18, 20, 21, 23
Pityrogramma–Pteris altissima type	20
Pleopeltis (*Microgramma*) *ciliata* (Polypodiaceae)	20
Polypodiaceae (–Blechnaceae–Pteridaceae)	7, 18
Polypodium	20, 22, 23
P. adnatum	20
P. aureum	18, 20
P. feullei	12
Pteridium (Dennstaedtiaceae)	17
Pteris (Pteridaceae)	21, 23, 31, 32
P. grandifolia type	20
Saccoloma domingense type (Dennstaedtiaceae)	20
S. elegans type	20
cf. *Schizaea* (Schizaeaceae)	20
Selaginella (Selaginelliaceae)	20, 23
S. anceps type	20
S. cf. *excurens*	32
S. sellowii type	20
Thelypteris (Thelypteridaceae)	20
T. pilosula	18

Gymnosperms

Araucaria angustifolia (Araucariaceae)	33
Cupressaceae	7, 32 (introduced)
Ephedra (Ephedraceae)	4, 5, 6, 7, 8, 11, 12, 13, 17
E. frustillata	2
Lepidothamnus (*Dacrydium*) *fonkii* (Podocarpaceae)	2, 9
Pilgerodendron type (Cupressaceae)	9, 12
Pinus (Pinaceae)	32 (introduced), 33
Podocarpaceae	15, 17, 18
Podocarpus (Podocarpaceae)	7, 8, 21, 22, 23, 24, 25, 28, 29, 31, 32, 33
P. nubigenus	2, 9, 12
Saxegothaea (Podocarpaceae)	7
S. conspicua	9, 12

Angiosperms

Acacia (Leguminosae)	7, 25, 30
Acaena–Polylepis (Rosaceae)	2, 8, 12, 13, 15, 17, 20, 21, 22, 23
Acalypha (Euphorbiaceae)	13, 14, 15, 17, 18, 20, 24, 30, 32
Acanthaceae (*Stenandrium*)	30
Acantholippia deserticola (Verbenaceae)	11
Acaulimalva purpurea (Malvaceae)	20
Acnistus (Solanaceae)	18
Adesmia (Leguminosae)	2, 8, 11
A. atacamensis	11
Aeschynomene (Leguminosae)	31
Aextoxicon (Aextoxicaceae)	12
Alchornea (Euphorbiaceae)	13, 14, 15, 16, 17, 20, 21, 28, 29, 30, 32, 33
Alestomeria [*Alstroemeria*?]	32
Alismataceae	7
Alismataceae (cf. *Sagittaria*)	13
Allophylus (Sapindaceae)	32
Alnus (Betulaceae)	7, 8, 13, 14, 15, 16, 17, 18, 21, 22, 23, 33
A. jorullensis	20
Alternanthera (Amaranthaceae; see also *Gomphrena*)	6, 8, 18, 20, 24, 25, 30, 31
Amaranthaceae (cf. *Gomphrena*)	13
Amaranthus type (Amaranthaceae) [chenoam]	8, 20
A. australis	25
A. dubius	25
Ambrosia (Compositae)	15, 17, 18, 24, 32
A. artemisioides	11
Anacardiaceae	13, 25, 30
Anacardium–Tapirira (Anacardiaceae)	30
Ananas (Bromeliaceae)	31
Anarthrophyllum (*A.* type, Leguminosae)	4, 8
Anatherostipa venusta (Gramineae)	11
Andira type (Leguminosae)	31
Antonia (Loganiaceae)	31
Apium type (Umbelliferae)	8, 32
Apocynaceae	13, 20, 25, 30
Araceae	32
Aragoa (Scrophulariaceae)	20
Araliaceae	25
Arenaria type (Caryophyllaceae)	8, 20
Aristida adscensionis var. *bromoides* (Gramineae)	11
Aristolochia (Aristolochiaceae)	31
Armeria maritima (Plumbaginaceae)	12
Arrabidaea (Bignoniaceae)	30
Artemisia (Compositae)	8, 20
Asclepidaceae	20
Astelia pumila (Liliaceae)	3, 12
Astronium (Anacardiaceae)	20, 30
Atriplex imbricata (Chenopodiaceae)	11
Avicennia nitida (Verbenaceae)	26
Ayenia (Sterculiaceae)	20
Azorella (Umbelliferae)	4, 8, 20
Baccharis (Compositae)	32, 33
B. boliviensis	11
B. tola	11
Baccharis type	8

Table 7.6. Representative Quaternary plant fossils from South America. *(Continued)*

Banara–Xylosma (Flacourtiaceae)	32
Barneoudia (Ranunculaceae)	12
Begonia (Begoniaceae)	14, 32
Beloperone (Acanthaceae)	20
Berberis (Berberidaceae)	2, 4, 7, 12
Bidens aff. *pilosa* (Compositae)	11
B. aff. *pseudocosmos*	11
Bignoniaceae	30
Bocconia (Papaveraceae)	14
B. integrifolia	20
Bomarea (Amaryllidaceae)	20
Bombacaceae	25
Bonamia (Convolvulaceae)	32
Boraginaceae	20
Borreria (Rubiaceae)	18, 29, 30, 32
B. anthospermoides	20
B. laevis	20
B. cf. *latifolia*	32
Bouteloua simplex (Gramineae)	11
Bravaisia (Acanthaceae)	25
Bromelia (Bromeliaceae)	30
Bromeliaceae	30
Bromus catharticus (Gramineae)	11
Brugmansia (*Datura–Methysticodendron*; Solanaceae)	20
Bursera (Burseraceae)	24, 25
Byrsonima (Malpighiaceae)	25, 29, 30
Cabralea (Meliaceae)	31
Cactaceae (cf. *Cereus*)	17, 30
Calandrinia (Portulacaceae)	8, 20
Calceolaria (Scrophulariaceae)	20
Calliandra (Leguminosae)	31, 32
Caltha (Ranunculaceae)	3, 9, 12
Calycera (Calyceraceae)	6
Campanulaceae (cf. *Rhizocephalum*)	13
cf. *Cardiospermum* (Sapindaceae)	20
Caryocar (Caryocaraceae)	30
Caryophyllaceae	2, 3, 4, 7, 9, 12, 13, 15, 20, 21, 22, 23, 31, 32
Cassia (Leguminosae)	20, 30, 31, 32
Castela type (Simaroubaceae)	25
Cavanillesia (Bombacaceae)	30
Cecropia (Urticaceae)	14, 16, 20, 21, 24, 25, 28, 29, 30, 32
Cedrela (Meliaceae)	20, 30
C. cf. *fissilis*	32
Celtis (Ulmaceae)	7, 14, 20, 24, 29, 30, 31, 32, 33
Ceratosanthes (Cucurbitaceae)	31
Cercophora type (Lecythidaceae)	8
Cereus (Cactaceae)	7, 30
Chamaesyce (Euphorbiaceae)	30
Chenoam	2, 3, 4, 5, 6, 7, 8, 12, 13, 15, 17, 20, 24, 32
Chlorophora (Moraceae)	25
Chorisia (Bombacaceae)	31
Chorizanthe commisuralis (Polygonaceae)	11
Chrysophyllum (Sapotaceae)	32
C. marginatum	32
Chuquiraga atacamensis (Compositae)	11
Cissus striata (Vitaceae)	12
Cistanthe (Portulacaceae)	11
Clarisia (Moraceae)	25
Cleome (Capparidaceae)	20
Clethra (Clethraceae)	13, 14, 20, 32, 33
cf. *Clusia* (Clusiaceae; see Guttiferae)	20
C. criuva	32
C. fossilia	26
Clusiaceae	13
Clusiaceae–*Calophyllum*	30
Cnidoscolus (Euphorbiaceae)	30
Combretum (Combretaceae)	30, 31
Compositae (Asteraceae)	5, 6, 9, 13, 15, 17, 18, 20, 21, 22, 23, 25, 30, 31
Compositae (*Ambrosia/Xanthium*)	6
Compositae (Asteroideae)	32
Compositae (Cichorioideae)	4, 6
Compositae (*Carduus* type)	6
Compositae (Liguliflorae)	2, 7, 12, 20, 32
Compositae (Mutisieae)	4
Compositae (Tubuliflorae)	2, 3, 4, 7, 12, 16, 20, 24, 29, 32
Condalia (Rhamnaceae)	7
Conocarpus erectus (Combretaceae)	26
cf. *Conomorpha* (Myrsinaceae)	20
Convolvulaceae	7
cf. *Conyza deserticola* (Compositae)	11
Copaifera (Leguminosae)	30, 31
Cordia curassavica (Boraginaceae)	30
C. lanata	20, 30
Coriaria ruscifolia (Coriaceae)	20
Cristaria (Malvaceae)	11
Crotalaria (Leguminosae)	8, 30
Croton (Euphorbiaceae)	18, 20, 32
C. bogotense (*C. bogotanus*) type	20
Cruciferae (Brassicaceae)	4, 6, 7, 8, 13
Cryptantha diffusa (Boraginaceae)	11
C. hispida	11
C. limensis	11
C. phaceloides	11
Cucurbitaceae	25
Cunoniaceae	31
Cuphea (Lythraceae)	20, 30, 31
C. cf. *ingrata*	32
C. cf. *urbaniana*	32
Curatella (Dilleniaceae)	30, 31
cf. *Cydista* (Bignoniaceae)	20
Cyperaceae	2, 3, 4, 6, 7, 8, 12, 13, 15, 16, 17, 18, 20, 21, 22, 23, 24, 25, 29, 31, 32, 33
Dalea (Leguminosae)	20
Dalechampia (Euphorbiaceae)	20
Daphnopsis (Thymelaeaceae)	20
D. cf. *beta*	32
Daucus type (Umbelliferae)	6
Desfontainia spinosa (Potaliaceae)	12
Dicliptera (Acanthaceae)	20
Dictyocaryum (Palmae)	14
Didymopanax (Araliaceae)	24, 29, 31, 32
Dioclea (Leguminosae)	30
Diplostephium meyenii (Compositae)	11
Dodonaea (Sapindaceae)	8, 15, 17, 23
D. viscosa	20
Donatia (*Avicennia*) *fascicularis* (Verbeniaceae, Saxifragaceae)	3, 12
Draba (Cruciferae)	20
D. hammenii	20
Drapetes muscosus (Thymelaeaceae)	9, 12
Drimys brasiliensis (Winteraceae)	20
D. granadensis	20
D. winteri	2, 3, 9, 12
Drosera (Droseraceae)	30, 31
Drymaria villosa type (Caryophyllaceae)	20
Dyckia (Bromeliaceae)	31
Eccremocarpus longiflorus (Bignoniaceae)	20
Echeveria (Crassulaceae)	20
Echinodorus (Alismataceae)	32, 33
Echinopsis atacamensis (Cactaceae)	11
Eichornia (Pontederiaceae)	33
Embothrium coccineum (Proteaceae)	2, 9, 12
Emmotum (Icacinaceae)	31
Empetrum (Empetraceae)	4, 7, 12
Empetrum–Ericaceae	3, 9, 12
Empetrum rubrum	2, 12

Table 7.6. Representative Quaternary plant fossils from South America. *(Continued)*

Encelia type (Compositae)	8
Epilobium (Onagraceae)	20, 23
Ericaceae	12, 13, 14, 15, 16, 17, 20, 21, 23, 30, 31, 32
Eriocaulon (Eriocaulaceae)	30
Eriocaulon–Paepalanthus	32, 33
cf. *Eriosema* (Leguminosae)	20
Eriotheca (Bombacaceae)	31
Eryngium (Umbelliferae)	32, 33
Erythroxylum (Erythroxylaceae)	30
Escallonia (Escalloniaceae)	17, 23
Eugenia (Myrtaceae)	20
Euphorbia (Euphorbiaceae)	11, 32
Euphorbiaceae	4, 7, 30, 31
Euphrasia (Scrophulariaceae)	9, 12
Euplassa (Proteaceae)	31, 32
Euterpe–Geonoma type (Palmae)	33
Evolvulus (Convolvulaceae)	20
Exodeconus integrifolius (Solanaceae)	11
Fabiana (Solanaceae)	11
Forsteronia (Apocynaceae)	30
Franseria type (Compositae)	8
Fuchsia (Onagraceae)	12, 20
F. regia	32
Gaiadendron punctatum (Loranthaceae)	20
Gaimardia australis (Centrolepidaceae)	12
cf. *Galium* (Rubiaceae)	11
Gaultheria ulei (Ericaceae)	32
Gentiana (Gentianaceae)	2, 12, 20, 21, 23
Gentianaceae	17
Geoffroea (Leguminosae)	7
Geraniaceae	7, 13
Geranium	12, 20, 21, 23
Gilia cf. *glutinosa* (Polemoniaceae)	11
Gnaphalium type (Compositae)	8
Gomphrena (Amaranthaceae)	25, 30, 31
Gomphrena–Pfaffia	32
Gramineae (Poaceae)	2, 3, 4, 5, 6, 7, 8, 9, 12, 13, 14, 15, 16, 17, 18, 20, 21, 22, 23, 24, 25, 28, 29, 30, 31, 32, 33
Griselinia (Griseliniaceae, Cornaceae)	12
G. cf. *ruscifolia*	32
Guapira (Nyctaginaceae)	32
Guarea (Meliaceae)	20
Gunnera (Gunneraceae)	2, 3, 7, 9, 12, 20
Halorag(id)aceae	7
Hancornia (Apocynaceae)	31
Hedyosmum (Chloranthaceae)	13, 14, 15, 16, 17, 20, 21, 22, 23, 30, 31
H. brasiliense	32
Helicteres (Sterculiaceae)	31
Heliocarpus (Tiliaceae)	20, 25
Heliotropium (Boraginaceae)	7
Hologyne macrogyne (Compositae)	11
Hibiscus (Malvaceae)	30
Hippocratea (Celastraceae, Hippocrateaceae)	30
Hoffmanseggia (Leguminosae)	11
Humiria (Humiriaceae)	30
Hydrangea serratifolia (Hydrangeaceae)	12
Hydrocotyle (Umbelliferae)	15, 20, 32, 33
Hymenaea (Leguminosae)	30
Hypericum (Guttiferae)	8, 20
Hyptis (Labiatae)	25, 30, 31, 32
Ilex (Aquifoliaceae)	16, 20, 21, 23, 28, 29, 30, 31, 32, 33
Inga (Leguminosae)	30
Ipomoea (Convolvulaceae)	25
Iridaceae	7, 13, 32
Jatropha (Euphorbiaceae)	30
Juglans (Juglandaceae)	7, 20, 21, 23, 25
Juncaceae	7, 20
Juncaginaceae	7
Junellia seriphioides (Verbenaceae)	11
Jungia type (Compositae)	33
Kielmeyera (Guttiferae)	31
Krameria lappacea (Krameriaceae)	11
Labiatae (Lamiaceae)	6, 7, 13, 32
Lafoensia (Lythraceae)	31
Lamanonia cf. *speciosa* (Cunoniaceae)	32, 33
Laplacea (Theaceae)	31
L. fruticosa	32
Lathyrus (Leguminosae)	20
Laurelia (Anterospermataceae, Monimiaceae)	12
Lebetanthus myrsinites (Epacridaceae)	12
Leguminosae (Fabaceae)	4, 8, 16, 25, 30, 31, 32
Leguminosae (Mimosoideae)	20, 29, 30, 32
Leguminosae (Papilionoideae)	6, 7, 20
Lentibulariaceae	30
Lenzia type (Portulacaceae)	8
Lepidium (Cruciferae)	11, 20
Lepidoceras kingii (Loranthaceae)	12
Leptocarpus chilensis (Restionaceae)	12
Lithraea–Schinus (Anacardiaceae)	32
Littorella australis (Plantaginaceae)	12
Lobelia tenera type (Campanulaceae)	20
Lomatia (Proteaceae)	7, 9, 12
Loranthaceae	20, 30, 32
Loricaria (Compositae)	17, 20
Lozanella–Trema (Ulmaceae)	15
Ludwigia (Onagraceae)	18, 20
Luehea (Tiliaceae)	30, 32
Lupinus (Leguminosae)	20
Lycopersicon chilense (Solanaceae)	11
Lysipomia (Campanulaceae)	20
Mabea (Euphorbiaceae)	30
Machaerium (Leguminosae)	30
Machaonia (Rubiaceae)	25
Macrocarpaea (Gentianaceae)	30
Macrolobium (Leguminosae)	25
Malpighiaceae	20
Malvaceae	4, 6, 13, 20, 30, 32
Malvastrum (Malvaceae)	23
Maprounea (Euphorbiaceae)	31
Mauritia (Palmae)	20, 31
Maytenus (Celastraceae)	2, 7, 9, 12
Melastomataceae	13, 16, 20, 24, 25, 30, 31, 32
Melastomataceae–Combretaceae	28, 29
Meliaceae	20, 31
Meliosma (Sabiaceae)	32
Merremia (Convolvulaceae)	20
Miconia (Melastomataceae)	15, 17, 20
Mimosa (Leguminosae)	30, 31, 32, 33
M. cf. *scabrella*	32
Mimusops preduplicata (Sapotaceae)	26
Misodendrum (Misodendraceae)	2, 3, 7, 12
Monni(n)a (Polygalaceae)	20, 21
Montia (Portulacaceae)	22, 23
M. fontana	20
M. meridensis	20
Moraceae–Urticaceae	8, 13, 14, 16, 20, 23, 28, 29, 31, 33
Moritzia lindenii (Boraginaceae)	20
Muehlenbeckia (Polygonaceae)	20
Mulinum (*M.* type, Umbelliferae)	4, 8
Munroa cf. *andina* (Gramineae)	11
M. decumbens	11
Mutisia (Compositae)	8, 20
Myrica (Myricaceae)	8, 13, 17, 20, 21, 23
Myriophyllum (Halorag(id)aceae)	2, 6, 7, 8, 12, 13, 15, 17, 20, 33
Myrsine (Myrsinaceae)	14, 15, 17, 29, 33
Myrtaceae	6, 7, 8, 9, 12, 14, 16, 20, 23, 25, 28, 29, 30, 31, 32, 33

Table 7.6. Representative Quaternary plant fossils from South America. *(Continued)*

Myrteola (Myrtaceae)	20
M. nummularia	3
Nanodea muscosa (Santalaceae)	2, 12
Nassauvia (Compositae)	4, 5
Nassella arcuata (Gramineae)	11
N. nardoides	11
N. pubiflora	11
N. pungens	11
Neea (Nyctaginaceae)	30, 31
Nothofagus (Fagaceae)	2, 3, 4, 7
N. dombeyi	9, 12, 20
N. obliqua type	12
Nymphaea (Nymphaeaceae)	30
Ocotea type (Lauraceae)	32
Oenothera (Onagraceae)	21, 23
O. multicaulis	20
Oleaceae	7
Onagraceae	2, 20
Opuntia camachoi (Cactaceae)	11
O. ignescens	11
O. sphaerica	11
Orchidaceae	7
Oreocereus (Cactaceae)	11
Oreopanax cf. *fulvum* (Araliaceae)	32
Orthrosanthus (Iridaceae)	20
Ouratea (Ochnaceae)	30, 31, 32
Ovidia (Thymelaeaceae)	12
Oxalidaceae	7
Oxalis (Oxalidaceae)	32
Paepalanthus–Eriocaulon (Eriocaulaceae)	20
Palmae	16, 20
Pamphalea (Compositae)	32, 33
Panopsis (Proteaceae)	20
Parastrephia quadrangularis (Compositae)	11
Passiflora (Passifloraceae)	20, 30
Pectocarya dimorpha (Boraginaceae)	11
Pera (Euphorbiaceae)	25, 32
Perezia (Compositae)	8, 12
Persea americana (Lauraceae)	26
Phacelia (*P.* type, Hydrophyllaceae)	6, 8, 11
Phaseolus (Leguminosae)	20
Phyllanthus (Euphorbiaceae)	18, 32
Phyllites oropouchensis (incertae sedis)	26
cf. *Pilea* (Urticaceae)	20
Piper (Piperaceae)	32
Piperaceae	16, 30
Piptadenia (Leguminosae)	32
Pisonia (Nyctaginaceae)	31
Pithecolobium unguis (Leguminosae)	26
Plantago (Plantaginaceae)	2, 4, 6, 7, 8, 12, 13, 17, 20, 21, 22, 23, 32
P. australis	20, 32, 33
P. hispida	11
P. rigida	15, 20
P. sericea	20
P. turficola	32, 33
Plenckia (Celastraceae)	30
Polygala (Polygalaceae)	4, 30, 32
Polygalaceae	31
Polygonaceae (cf. *Rumex*/*Ruprechtia*)	13
Polygonum (Polygonaceae)	7, 18, 20
Polylepis (see *Acaena*/*Polylepis*)	
Pontederia (Pontederiaceae)	30
Pontederiaceae	31
Portulacaceae	23
Potamogeton (Potamogetonaceae)	15, 31
Pouteria (Sapotaceae)	30
Primulaceae	7
Prosopis (Leguminosae)	4, 7
Proteaceae	16, 20, 23, 31
Protium (Burseraceae)	25, 30
Prunus type (Rosaceae)	32
Pseudopanax laetevirens (Araliaceae)	9, 12
Psychotria (Rubiaceae)	32
P. cf. *alba* (Rubiaceae)	32
Pterocarpus–Sclerolobium (Leguminosae)	30
Puya (Bromeliaceae)	17, 20
Quercus (Fagaceae)	20
Quinchamalium (Santalaceae)	12
Ranunculaceae	2, 6, 7, 12, 13
Ranunculus (Ranunculaceae)	8, 20
R. cf. *bonariensis*	32
Rapanea (Myrsinaceae)	20, 21, 24, 25, 30, 31, 32
Relbunium (Rubiaceae)	20, 32
Rhamnus type (Rhamnaceae)	32
Rhaphithamnus spinosus (Verbenaceae)	12
Rhizocephalum (Campanulaceae)	23
R. candollei	20
Rhizophora (Rhizophoraceae)	28
R. mangle	26
cf. *Rhus* (Anacardiaceae)	20
Ribes (Grossulariaceae, Saxifragaceae)	2, 7, 12
R. magellanicum	3
Rosaceae	4, 7, 20
Roupala (Proteaceae)	31, 32
Rubiaceae	2, 4, 6, 7, 12, 20, 30, 32
Rubiaceae (cf. *Borreria*)	13
Rumex (Polygonaceae)	2, 4, 7, 15, 21
R. tolimensis	20
Ruppia (Potamogetonaceae)	8, 24
Rutaceae	30
Rutaceae–*Eisenbeckia*	30
Sagittaria–Echinodorus (Alismataceae)	20, 30
Salacia (Celastraceae)	31
Salicaceae	7
Salpichroa type (Solanaceae)	8
Salvia killipiana type (Labiatae)	20
S. type	8
Sapindaceae	30
Sapium (Euphorbiaceae)	20, 30
Satureja nubigena type (Labiateae)	20
Schinus (Anacardiaceae; see also *Lithraea*, *Schinus*)	4, 6, 7
Schkuhria multiflora (Compositae)	11
Scirpus (Cyperaceae)	17
Sclerolobium (see *Pterocarpus–Sclerolobium*)	
Scrophulariaceae	7
Scybalium (Balanophoraceae)	20
Sebastiana (Euphorbiaceae)	30
S. brasiliensis (Euphorbiaceae)	32
S. commersoniana	32
S. cf. *schottiana*	32
Senecio (Compositae)	8, 32, 33
S. aff. *atacamensis* (Compositae)	11
Sericotheca argentea (Rosaceae)	20
Serjania (Sapindaceae)	30, 32
Sessea (Solanaceae)	20
Sida (Malvaceae)	25
Simarouba (Simaroubaceae)	30
Sisymbrium philippianum (Cruciferae)	11
Sisyrinchium (Iridaceae)	20
Smilax (Smilacaceae)	31
Solanaceae	4, 6, 7, 8, 13, 20, 30, 31
Solanum (Solanaceae)	8, 32
Spergularia (Caryophyllaceae)	11
S. type	6
Spondias (Anacardiaceae)	24, 25
Stenandrium (see Acanthaceae)	
Stipa chrysophylla (Gramineae)	11
Struthanthus (Loranthaceae)	32
Stryphnodendron (Leguminosae)	30, 31
Styloceras laurifolium (Buxaceae)	20

Table 7.6. Representative Quaternary plant fossils from South America. *(Continued)*

Styrax (Styracaceae)	31, 32
S. rosadoi	27
Symphonia (Guttiferae)	16, 30
Symplocos (Symplocaceae)	20, 31
S. lanceolata type	32
S. tenuifolia type	32
Tabebuia (Bignoniaceae)	30
Tagetes multiflora (Compositae)	11
Tapirira (Anacardiaceae; see also *Anacardium–Tapirira*)	25, 32
Tarasa operculata (Malvaceae)	11
T. type	8
Tepualia stipularia (Myrtaceae)	12
Tetroncium magellanicum (Cyperaceae; Juncaginaceae)	2, 3
Tetrorchidium rubrivenium (Euphorbiaceae)	32
Thalictrum (Ranunculaceae)	8, 17
T. podocarpum	20
Tiliaceae	16, 20
Tiquilia atacamensis (Boraginaceae)	11
Tournefortia (Boraginaceae)	20
Trechonaetes (Solanaceae)	8
Trema (Ulmaceae)	14, 24, 25, 32
Tribulus (Zygophyllaceae)	25
Trichilia (Meliaceae)	30, 31, 32
Trifolium type (Leguminosae)	8
Trigonia (Trigoniaceae)	32
Tristerix (Loranthaceae)	12, 20, 32
T. longebracteatus type	20
Trixis (Compositae)	32
Typha (Typhaceae)	6, 7, 20, 25, 31
T. angustifolia	8, 24
T. domingensis	32
Ulmaceae	20
Ulmaceae (cf. *Trema/Lozanella*)	15
Umbelliferae (Apiaceae)	2, 3, 6, 7, 8, 9, 12, 13, 15, 17, 20, 21, 23, 30, 31, 32, 33
Urmenetea atacamensis (Compositae)	11
Urticaceae, Urticaceae/Moraceae	6, 7, 8, 30, 32
Urticales	15, 17, 22, 23
Urvillea (Sapindaceae)	20, 32
Utricularia (Lentibulariaceae)	20, 32
Valeriana (Valerianaceae)	2, 9, 12, 13, 15, 17, 20, 21, 23
V. arborea type	20
V. stenophylla type	20
V. triphylla type	20
Valerianaceae	32
Vallea (Elaeocarpaceae)	13, 14, 20
Vellozia (Velloziaceae)	30, 31
Verbena (Verbenaceae)	32
Verbenaceae	4, 6, 8
Vernonia (Compositae)	32
Viburnum (Caprifoliaceae)	20
Vicia (Leguminosae)	20
Villaresia (Celastraceae)	31
Viola (Violaceae)	20
Vismia (Guttiferae, Clusiaceae)	20
Warszewiczia (Rubiaceae)	20
Weinmannia (Cunoniaceae)	15, 16, 20, 23, 32, 33
W. trichosperma (Cunoniaceae)	9, 12, 13, 17
Xylosma (see *Banara–Xylosma*)	
Xyris (Xyridaceae)	32, 33
Zanthoxylum (Rutaceae)	18, 30, 32
Zea mays (Gramineae)	15, 32 (introduced)
Zizyphus (Rhamnaceae)	30

been reconstructed with subdecadal resolution. There was a mid-Holocene thermal maximum, and fluctuations during the last 5400 years include a Little Ice Age between 3800 and 2800 years B.P. The principal cause for these changes is attributed to shifts in the ITCZ. The chronology suggests correlation and teleconnections with events in the high-latitude Northern Hemisphere. Similar results were achieved using leaf wax buildup as biomarkers for vegetation change between 15,000 and 10,000 years B.P. (Hughen et al., 2004). However, there was the caveat, important to unraveling the complex environmental and vegetation history at this high level of resolution, that vegetation lagged behind climatic events in the basin by several decades.

Much of this context information is summarized by Lea et al. (2003) as follows:

> "A high-resolution western tropical Atlantic sea surface temperature (SST) record from the Cariaco Basin on the northern Venezuelan shelf, based on Mg/Ca values in surface-dwelling planktonic foraminifera, reveals that changes in SST over the last glacial termination are synchronous, within ±30 to ±90 years, with the Greenland Ice Sheet Project 2 air temperature proxy record and atmospheric methane record. The most prominent deglacial event in the Cariaco record occurred during the Younger Dryas time interval, when SSTs dropped by 3° to 4°C. A rapid southward shift in the atmospheric intertropical convergence zone could account for the synchroneity of tropical temperature, atmospheric methane, and high-latitude changes during the Younger Dryas." (p. 1361)

One result of particular interest for ecosystem evolution arising from these multidisciplinary studies is the frequent association of the cold-dry and warm-moist components of the climate in the lowlands adjacent to the Amazon Basin. Another is that collectively the data bolster the relatively meager information available from direct paleobotanical and palynological approaches.

A site where Quaternary lowland vegetation has been studied is Lake Valencia (403 m elevation), a putative Pleistocene refugium for the Neotropical rain forest (Vanzolini & Williams, 1970; Prance, 1973, 1982; Brown et al., 1974). Geological studies (Schubert, 1979) indicate, however, that dry conditions prevailed during glacial times, and this is supported by the paleobotanical record (Salgado-Labouriau, 1980; Bradbury et al., 1981; Leyden, 1985). The plant microfossil assemblages also indicate subhumid conditions in the cold intervals of the Pleistocene, more mesic conditions in the early Holocene, then a variable MAP in the middle and late Holocene but generally drier with a moist period between 5200 and 2200 years B.P. In the Late Glacial (~13,000 years B.P.), Lake Valencia was a saline marsh surrounded by savanna that gave way to a dry

lower montane forest at 9800 years B.P., then semi-evergreen and deciduous forest with abundant *Brosimum* at 9500 years B.P. By 8300 years B.P., essentially modern vegetation existed at the site. The composition of the fossil flora is given in Table 7.6 (Ref. 24). One of the important messages from the Lake Valencia studies is that a good part of the Late Glacial was cold and dry.

The tepuis—Very little paleobotanical information is available on the Quaternary climates and vegetation of these structures in Venezuela. It may be assumed that it was drier and cooler than in the lowlands, given the exposure 4000 m above the surroundings, with moist habitats in depressions where water accumulated. Rull (1991; Rull et al., 2005) believes on the basis of spore and pollen assemblages that the environments were arid to semiarid before the Holocene. This is supported by radiocarbon dates indicating that peat formation was not extensive prior to ~8000 years B.P. (Schubert & Huber, 1989; Schubert et al., 1992). Slight changes in moisture are indicated by vegetation alternating between herbaceous and shrub-forest (viz., replacement of *Stegolepis* meadows by *Bonnetia* forests). Four levels of river terraces, cut into the alluvium at the base of the tepuis during floods, indicate variability in Holocene precipitation. For the past 6000 years the prominent vegetation has been highland meadows (Rull, 2005).

Venezuelan Andes—Several studies have been made on the Quaternary vegetation of the high altitudes in Venezuela (Salgado-Labouriau, 1984, 1986, 1987/1988, 1991a, b; Rull et al., 1987; Salgado-Labouriau et al., 1992). These are mostly from Late Glacial and more recent deposits, and there are no extensive cores extending the record back into earlier glacial times (Salgado-Labouriau et al., 1988; Rull, 1998). In general, the records from the Venezuelan and Colombian Andes are similar, including various stadials (El Caballo and Fúquene, respectively), changes in tree line, and fluctuations between forest and páramo.

A few plants of presumed Pleistocene age are described by Berry (1925e) from the Oropouche Formation of Trinidad, and these are listed in Table 7.6.

Brazil

Megafossils of Quaternary age are rare for Brazil. They include leaves probably of Pleistocene age described as *Styrax rosadoi* (Styracaceae) from Olho d'Agua do Vieira, Município de Russas, state of Ceará, and late Pleistocene petrified wood of *Astronioxylon mainieri* (Anacardiaceae), *Matayboxylon tietense* (Sapindaceae), *Myrocarpoxylon sanpaulense* (Fabaceae, Papilionoideae), *Piptadenioxylon chimeloi* (Fabaceae, Mimosoideae), and *Qualeoxylon itaquaquecetubense* (Vochysiaceae) from alluvial deposits of the Tietê River at São Paulo.

Microfossil assemblages of Quaternary age have been described from numerous sites in Brazil, although the vast extent of the country and the complexity of the vegetation dilute the database considerably for reconstructing details of its history. Examples of studies are given below for the northern, central, and southern portions of the country, and for the mosaic of drier vegetation types that characterize large expanses of the landscape.

Northern Brazil—Plant microfossils of Quaternary age from the lowlands of northern Brazil indicate that cold and dry climates prevailed at the LGM, changing to warmer and moister conditions toward the Late Glacial–Holocene (Behling, 2002a, b, Lagoa da Confusão, state of Tocantins; Behling et al., 2000, GeoB 3104-1 core, upper continental slope, northeastern Brazil, >42,000 years B.P.; Ledru et al., 2001, Lagoa do Caçó, Maranhão State, 2°58'S). The period between 15,500 and 11,800 years B.P. was very moist as suggested by increases in pollen of *Podocarpus* and *Hedyosmum* (Haberle & Maslin, 1999). Dating of speleothems and plant remains by ^{230}Th mass spectrometry indicates that forest periodically existed in the Quaternary in presently semiarid northeastern Brazil (Auler et al., 2004). At these times, there were likely opportunities for exchange between the Atlantic and Amazon rain forests. Later short-term fluctuations correlate with Heinrich and D–O events to the north, reflecting strong teleconnection between climates of the high latitudes and those at 3°40'S. Later in the Holocene, the effects of fluctuating sea levels on lowland terra firme (unflooded) and várzea and igapó (flooded) vegetation (Chapter 3, Brazil) are evident in a core from the Rio Curuá (state of Pará, 1°30'S) in the eastern Amazon Basin with sediments dating back to >8000 years B.P. (Behling & Lima da Costa, 2000). Before that time, there was an active flowing (widespread várzea, igapó; veredas or *Mauritia* palm swamps) and afterward a more passive river system (widespread terra firme). At 2740 ^{14}C years B.P., the river was blocked, creating flooded conditions over terra firme habitats. This history documents that parts of the supposedly stable, unflooded terra firme sites were inundated during the Holocene due to climate changes and to alterations in the physical environment. Charcoal increases in the Rio Curuá region about 3000 ^{14}C years B.P. reflect human presence. The influence of fluctuating sea levels in the Holocene is also evident in a core from Lago do Aquiri (state of Maranhão, 3°10'S) as the Atlantic Ocean periodically extended farther inland (Behling & Lima da Costa, 1994).

A similar sequence is shown in the Barreirinhas region of Maranhão State around Lagoa do Caçó (Pessenda et al., 2004). Carbon isotopes and charcoal analyzed from restinga (coastal vegetation), forest, cerrado, and cerradão provide a record back to 15 ^{14}C Kyr B.P. Between 15,000 and 9000 ^{14}C years B.P., forest was present and grew under humid conditions. Between 9000 and 3000 ^{14}C years B.P., savanna expanded and toward the end of the interval charcoal increased, indicating a dry climate, fires, and human disturbance. After 3000 ^{14}C years B.P., humid conditions prevailed, with the forest showing increasing human impact. Studies on the Bragança Peninsula, Pará, northern Brazil, indicate low levels of inundation and dry conditions corresponding to the Little Ice Age in this part of the Brazilian lowlands (Cohen et al., 2005).

Central and southern Brazil—This region (e.g., Laguna Campestre [Salitre], Minas Gerais State, 19°S; Ledru, 1993; Ledru et al., 1996; Fig. 7.122) is susceptible to avected south

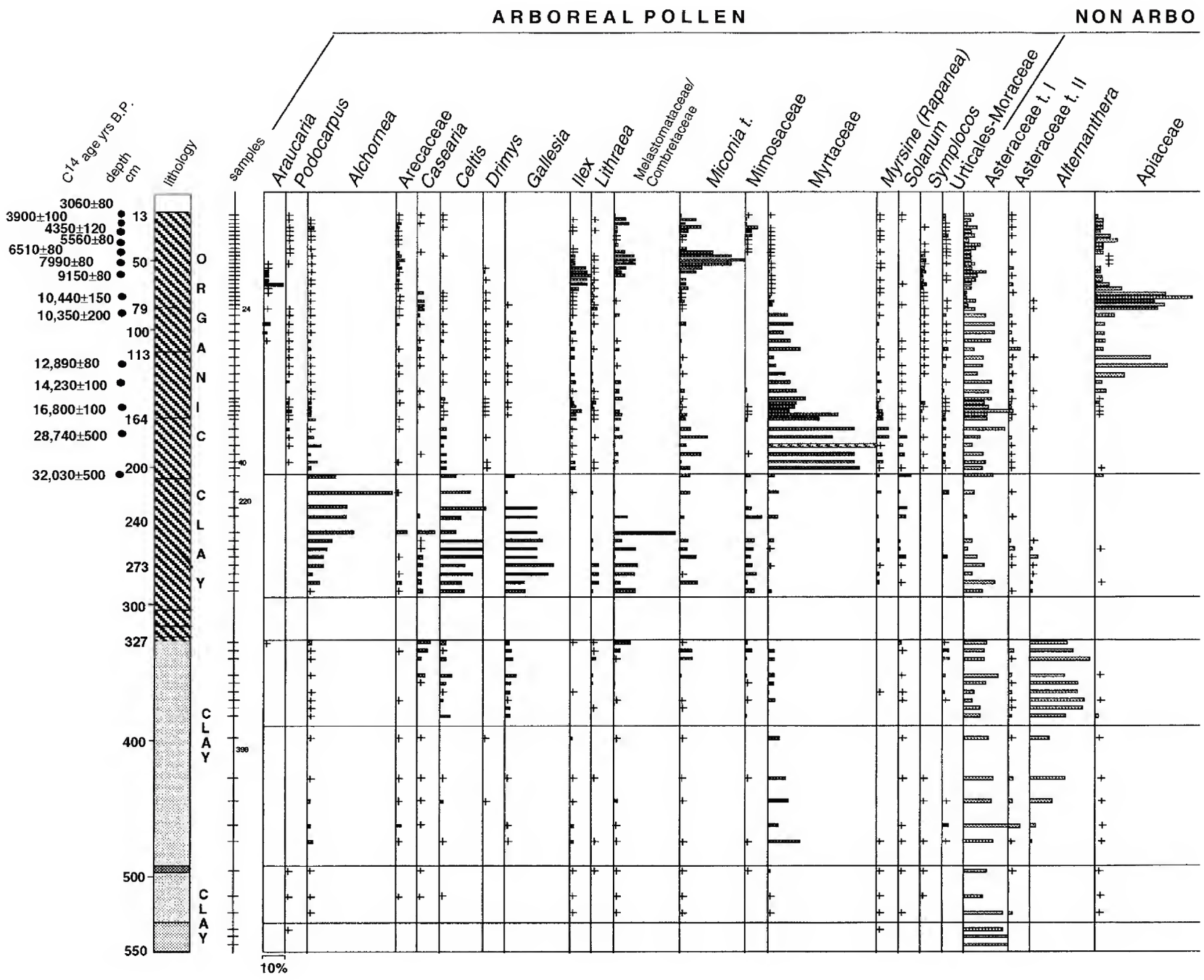
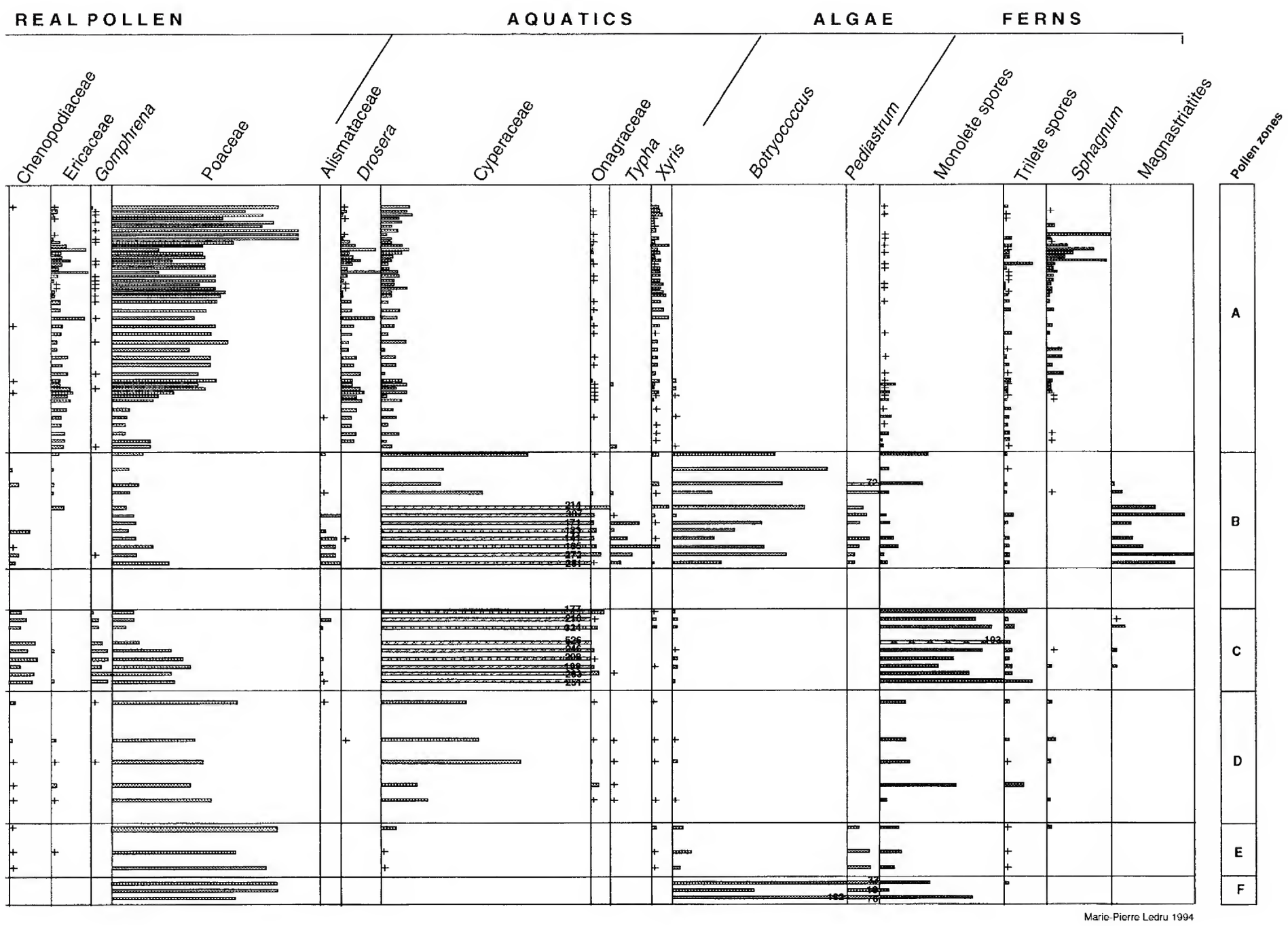


Figure 7.122. Spore and pollen percentage diagram from core Salitre LC3, southern Brazil. + = percentages <1%. Reprinted from Ledru et al. (1996), with permission of Elsevier Science Publishers, Amsterdam. (*Continued on facing page.*)

polar air in the austral winter, which causes periodic cold, fog, and moist conditions in the lowlands (Chapter 1, Brazil), with warmer temperatures maintained on the slopes and in the uplands. Tropical air masses prevail in the austral summer, and the shifts are caused by the annual migration of the ITCZ. The potential vegetation is warm/moist-habitat *Araucaria* forest, and cooler/drier-habitat semi-deciduous forest–cerrado, with gallery forest along the rivers and Atlantic rain forest extending inland ~350 km from the coast. Between 50,000 and 40,000 years B.P. it was dry, followed by a moist interval peaking at 35,000 years B.P. Between 10,000 and 7000 years B.P., there was reduced sedimentation, and where pollen is preserved, it represents xerothermic vegetation (Ledru et al., 1998). At 7000–4000 years B.P., there was greater moisture as shown by expanded semi-deciduous, swamp, and gallery vegetation. There were subsequent moist-dry and cool-warm fluctuations continuing until 4000–3000 years B.P., when modern conditions were established. Other studies in the area further document the changing climate and vegetation, including periods of absent or highly modified Atlantic, *Araucaria*, and cloud forests during the Late Glacial period 35,000–17,000 years B.P. (colder and drier; Behling, 1997a, b), a possible Younger Dryas (Behling, 1995) and Little Ice Age event (Behling et al., 2004; *Araucaria* forests disappear), and mid-Holocene dryness with depleted human populations (Araujo et al., 2005).

Near Brasília (Distrito Federal, 15°34'S), cores reveal similar sequences (Ferraz-Vicentini & Salgado-Labouriau, 1996; Salgado-Labouriau et al., 1998; Barberi et al., 2000): >30,000 years B.P., little deposition (dry conditions); 30,000 years B.P., peat begins to form, and between 25,790 and 24,200 years B.P. there was a marsh with gallery forest, and cerrado on the drier sites; 24,000–21,450 years B.P., humid and cooler (no veredas); 21,000–7220 years B.P., a dry phase; 7000 years B.P., the palm swamp (vereda) begins to form and after 5600 years B.P., versions of the modern vegetation (cerrado, gallery forest, palm swamp) appear.

Dry plant formations (shrublands/woodlands [seasonally dry tropical forests], caatinga [driest, stunted, transitional to the woodlands often with a spiny component], cerrado [savanna], campos [grasslands])—Climates favorable for dry vegetation began developing and expanding mostly in about the middle Miocene, while suitable habitats were locally available before that time due to slope, exposure, and edaphic conditions. They expanded during the cool dry intervals of the late Neogene



and especially the Pleistocene, and have been maintained, highly modified, and further expanded by human activity particularly through the use of fire. The dry vegetation types of South America are discussed by Pennington et al. (2000), and the present distribution of cerrado in Brazil is shown in Fig. 3.147.

Seasonally dry tropical forests grow mostly on fertile soils in areas where MAP is <1600 mm, in areas that receive <100 mm five to six months of the year, and in areas where the trees are deciduous in the dry season. Prominent families include Fabaceae and Bignoniaceae, together with Anacardiaceae, Capparidaceae, Euphorbiaceae, Flacourtiaceae, Myrtaceae, Rubiaceae, and Sapindaceae, with Cactaceae and a limited number of grasses in the understory. Pennington et al. (2000, fig. 1) conclude that the most parsimonious explanation for the present distribution of dry vegetation in the Neotropics is cooler and drier Quaternary climates at the low and mid-elevations. Rain forest and moist montane plants grew mostly as gallery forests and in western Amazonia (see Chapter 8, Refugia).

The pollen signature of the cerrados includes Poaceae (to 74%; Salgado-Labouriau, 1973) and other types (*Borreria*, *Byrsonima*, *Caryocar*, *Curatella*, *Didymopanax*, *Qualea*, *Vellozia*) that allow recognition of the plant formation when well developed over a sizable area. In a review of cerrado history, Ledru (2002) notes that this vegetation, along with gallery forests and palm swamps, is represented in sediments dated at >32,000 years B.P. from central Brazil (Cromínia, Goiás; Salgado-Labouriau et al., 1997), and that the sediments include charcoal, indicating that fire was a factor prior to human disturbance. In pre-full glacial times, there was either grassland where forests exist today, or forest and savanna alternated both north and south of the equator, indicating periodic dry conditions. In the full glacial (32,000–24,000 years B.P.), savanna was replaced by grassland in the south, and between 18,500 and 11,500 years B.P. it was very dry at the Goiás site, while in the Late Glacial (11,500 years B.P. in the north and 16,000–14,000 years B.P. in the south), warmer and moister conditions began to develop. Climate fluctuations in the Holocene are reflected in carbon isotopes in soils from Amapá, Alter do Chão, and Roraima (Sanaiotti et al., 2002). These sites are presently isolated cerrado within the forest and remained so in the Holocene, while presently forested localities at Humaitá and Carolina show profiles indicating drier woody savanna in the early Holocene. This result from carbon isotope studies is consistent with that from a broader north–south transect of spore and pollen profiles through savanna regions of South America (7°N to 20°S; Behling & Hooghiemstra, 2001). The early Holocene (to 6000–5000 years B.P.) was drier and savanna expanded.

Behling and Hooghiemstra (2001) attribute the climatic fluctuations and the vegetation responses to latitudinal migrations of the ITCZ. Cerrado in approximately modern dress appears ~10,000 years B.P. in northern Brazil and ~7000 years B.P. in central Brazil (Ledru, 2002).

The limited evidence on the history of caatingas vegetation reflects a similar climate sequence (De Oliveira et al., 1999). Palynomorphs dating back to 10,900 years B.P. were obtained from a bog in the Icatu River Valley, middle São Francisco River system (10°24'S) in northeastern Brazil. In the lower parts of the sequence, dating to 10,900–10,540 years B.P., the vegetation included elements of the present Amazonian and Atlantic Rain Forest (moist conditions, as above). Similar conditions continued from 10,520–6790 years B.P. with an increase in *Mauritia* pollen suggesting warming, then caatingas–cerrado at 8910–6790 years B.P. indicating drying. The interval from 6790–6230 years B.P. lacks palynomorphs, possibly due to a very dry climate, and between 6230 and 4535 years B.P. a mosaic of gallery forest, cerrado, and caatinga is established, leading to the modern vereda (*Mauritia vinifera* palms) bordered by semi-deciduous forest.

The Quaternary history of grasslands in southern and southeastern Brazil is reviewed by Behling (1997a, b, 2002b; Behling et al., 2004). During pre- and early full-glacial times, the lower elevations were occupied by semi-deciduous forest and cerrado that were replaced later in the full glacial by grassland. In the upper elevations of the Brazilian highlands, *Araucaria* forests were confined to valley bottoms and elsewhere were replaced mostly by grassland. The Atlantic Forest was reduced in extent and replaced by cold-adapted forests and expanded grasslands. Thus, grasslands were prominent in southern and southeastern Brazil in areas that today are occupied by a mosaic of different forest types. During the full glacial, the MAT is estimated at 5°–6° C cooler than at present (to possibly as much as 10° C cooler in the highlands of Cambará, Rio Grande do Sul; Behling et al., 2004), and conditions were dry. The grasslands were replaced by the modern *Araucaria* forests in the late Holocene ~3000 ^{14}C years (4320 calendar years) B.P. and especially by 1500–1000 calendar years B.P.

The inference that climates were both cold and dry in parts of Brazil during intervals of the Quaternary, and that the plant formations responded by (a) expansion of dry vegetation types and (b) restriction of moist vegetation types more to gallery forests and river valleys, is provided by several other studies (Behling & Lichte, 1997; Behling, 1998; Salgado-Labouriau et al., 1998; Lichte & Behling, 1999). The overall conclusions are reflected in the summary of a spore/pollen and charcoal record 48,000–18,000 ^{14}C years B.P. near the village of Catas Altas, southeastern Brazil, by Behling and Lichte (1997, p. 348):

> "The last-glacial landscape was covered by extensive areas of subtropical grasslands and small areas of gallery forests along the rivers, where tropical semideciduous forests and cerrado ecosystems exist today. The subtropical gallery forests were composed of *Araucaria* forest trees such as *Araucaria angustifolia*, *Podocarpus*, *Drimys*, *Ilex*, and *Symplocos*. Paleofires were frequent. The record indicates that subtropical grassland vegetation, which today is found in patches on the highlands in southern Brazil (especially in the state of Santa Catarina), expanded from southern Brazil to southeastern Brazil, over a distance of more than 750 km, from latitudes of about 28° S to at least 20° S. The completely different last-glacial environment, in comparison to the present-day environment, reflects a dry and cold climate with strong frosts during the winter months. Temperatures of 5°–7°C below those of the present are inferred for the last glaciation."

The unsettled climatological meaning of stonelines (buried accumulations of stones and gravel; Pennington et al., 2000) is addressed by Lichte and Behling (1999). Ab'Saber (1982) originally suggested that these features were of Quaternary age and developed only under dry climates, but this has not been established in all cases. Lichte and Behling (1999, p. 341) note, however, that "there is clear mineralogical and granulometrical contrast between bedrock and the sediment cover on top of stonelines, and finally the position of stonelines between the weathered bedrock and the sediment cover on the top of isolated hills proves as definitely as all the other aspects that the sediment cover consists of largely wind-transported material. Thus the modern landscape presents forms influenced by the dry and cold climatic conditions that all the evidence has proved." The point is that, for the moment, the association of stone lines with dry climate cannot be summarily dismissed.

Pantanal—There is insufficient paleobotanical and paleopalynological evidence to reconstruct the history of the Pantanal plant formations directly, and inferences must be made from ancillary lines of evidence, regional context information, and global trends. The vegetation is generally regarded as having passed through a series of successional stages (Por, 1995, p. 42) from disruptions caused by late Neogene and Quaternary changes in climate (cooling, drying) and in the physical environment (drainage patterns, water tables, enhanced salinity from higher sea levels). It is assumed that, during the many cool-dry intervals and lower sea levels of the Quaternary, elements of the semiarid Gran Chaco vegetation expanded into the Pantanal, and retreated during the warmer-wetter phases and higher sea levels (mid-Pliocene, Quaternary interglacials). The presence of paleodunes supports the occurrence of one or more dry periods (Klammer, 1982). A propitious time for the origin of the modern Pantanal, therefore, would be in about the middle Pliocene, although direct evidence is lacking. What is more certain is that this fragile and delicately balanced ecosystem has had a very dynamic history that documents its susceptibility to perturbation.

Atlantic forests—A period of maximum Cenozoic warmth, abundant moisture, expanding terrestrial habitats from draining Cretaceous epicontinental seas, and the appearance of an

increasing number of lineages that are morphologically and presumably ecologically similar to modern taxa make plausible environments for the assemblage and radiation of a more or less modern Neotropical rain forest from Late Cretaceous progenitors. These conditions came together in the LPTM–EECL interval of the Paleogene and especially by the middle Eocene. The Brazilian Highlands were already present, so the beginnings of the Atlantic forests as geographically separate from the Amazon forests probably date from about the same time, although the extent of coastal habitats was less because of the higher sea levels. Even if greater moisture and less seasonality prevailed at this time, the exposed portions of the highlands would still be drier than the lowlands on either side because of edaphic, slope, and exposure factors.

There is a formidable gap between these assumptions on the origin of the Atlantic forests and the direct evidence for their subsequent history that begins with the last glacial and Holocene (Ledru et al., 2005). It is worthwhile to recall that both the Atlantic and Amazon forests are mosaics of forest types, with the lowland rain forest being prominent among several other components. Thus, accounting for "the" forest requires attention to the drier as well as the wet-habitat communities. The onset of cold-dry glacial and mid-Holocene intervals intensified the highland barrier, covered more by shrubland and grassland, and these were the times of greatest isolation and reduction in the extent of the rain forest (Behling, 1997a, b, 2002a; Behling & Lichte, 1997). They also were times when drier components of more open habitats, such as *Cecropia*, could more easily cross the barrier to the rain forest. Studies on the vegetation and environmental history of the lowland Neotropical forests have demonstrated that they experienced both kinds of climates (cool, dry; warm, wet) during the Quaternary and responded to those changes by modifications in the range and composition of the various component plant formations and associations. The interval between 15,500 and 11,800 years B.P. was especially moist in the region (Haberle & Maslin, 1999), and humid conditions continued until ~6790 years B.P. (De Oliveira et al., 1999). There were moist periods at 4320 years B.P., and the modern conditions have prevailed since ~1500 years B.P. The moist climates would have favored maximum extent and greater opportunity for exchange of rain forest elements between the Atlantic coast and Amazonia, especially along lowland passages through the highlands. The same changing sequence of cool-dry and warm-moist climates prevailed throughout the latter part of the Neogene and the 2.6 Ma of the Quaternary. Until additional evidence is available, it is assumed that the present angiosperm-dominated Neotropical rain forest became recognizable as a formation during the LPTM–EECL, it was already segregated into Amazonian and Atlantic sectors by the late Eocene, and that these have varied but remained distinct throughout the climatic turmoil of the Neogene and Quaternary.

Archeology—Prous and Fogaça (1999) believe there is credible evidence for humans (Lagoa Santa people) in central Brazil 14,000–10,000 years B.P., and Behling (1996) cites high charcoal concentrations as indicating human presence in the state of Pará ~10,800 years B.P. These were hunters and gatherers and apparently had limited effect on the vegetation. The question of "how virgin is virgin rain forest" has been getting a lot of press in efforts to determine the potential recoverability of the forest from human impact that is presently causing a loss estimated at 6 million ha/yr (Willis et al., 2004; Hambler, 2004; Beehler et al., 2004). The question also relates to how long Neotropical vegetation has been altered by humans as well as by climatic and geologic factors (Chapter 6, Panama, Quaternary). As summarized by Willis et al. (2004), in the central Amazon Basin, soils with high fertility enhanced by burning and agriculture (terra preta) date from at least 2500 years B.P., and in the Upper Xingu region of Brazil there are extensive late prehistoric settlements between 1250 and 1600 years old.

Fine Tuning—In Chapter 6, evidence for a Younger Dryas and other Quaternary events, first demonstrated for the northern high latitudes, were summarized for northern Latin America to about latitude 9°N. They are also being recognized in South America, and those mentioned in the text are arranged below from north to south:

Venezuela ~9°–10°N, Younger Dryas, mid-Holocene warm period, Little Ice Age;

Colombia ~4°–5°N, Younger Dryas (Santa Isabel moraines, Cordillera Central, 13,810–8040 calendar years B.P. [11,490 ± 60 and 7440 ± 70 ^{14}C years B.P.]; Thouret et al., 1996; van der Hammen & Hooghiemstra, 1995);

Brazil ~3°–4°N, Younger Dryas, Heinrich and D–O events, Little Ice Age;

Ecuador ~3°–4°S, Younger Dryas (Portreillos readvance, Eastern Cordillera, ~13,120 and 11,260 calendar years B.P. [10,860 and 10,040 ^{14}C years B.P.]; Clapperton et al., 1997); (Ricu Pichincha M6 terminal moraine, 12,600 and 10,200 calendar years B.P. [~10,600 and 9000 ^{14}C years B.P.]; Heine & Heine, 1996); (Cordillera of Ecuador, Peru, and Bolivia and the Patagonian ice cap; Osborn et al., 1995);

Galápagos Islands, 0° (equator, insular), possibly mid-Holocene dry period;

Peru ~8°S, mid-Holocene dry period, Little Ice Age;

Bolivia ~15°S, Younger Dryas (western slope Cordillera Real, basal organic lake sediments, 10,240 and 9540 calendar years B.P. [8810 ± 110 and 8980 ± 70 ^{14}C years B.P.]; eastern slope 9680–9440 calendar years B.P. [8550 ± 70 ^{14}C years B.P.]; Abbott et al., 1997a, b, 2000); also mid-Holocene dry period, Heinrich events 1 and 2; and

Southern Argentina–Chile (Patagonia) ~45°S, mid-Holocene warm, dry interval; Younger Dryas (but see Markgraf, 1991; Bennett et al., 2000), Little Ice Age.

Central Amazonia (~15°–25°S)—The vegetation history of this part of Brazil segues into the subject of refugia. The relevant aspects that can be addressed from the paleopalynological database are (a) the extent to which the vegetation of central Amazonia and the surrounding lowland regions was

altered during the Quaternary, given that much of the direct information comes from the Late Glacial and Holocene, while virtually nothing is known about the previous glacial and interglacial periods; (b) whether the causal factors involved cooling, or both cooling and drying as seems to be the case; and (c) if so, whether drying was sufficient to disrupt the rain forest and allow intervening areas to become occupied by drier vegetation. These and other synthesis questions are addressed in the following chapter.

REFERENCES

Abbott, M. B., M. W. Binford, M. Brenner, and K. R. Kelts. 1997a. A 3500 ^{14}C yr high-resolution record of water-level changes in Lake Titicaca, Bolivia/Peru. Quatern. Res. 47: 169–180.

———, G. O. Seltzer, K. R. Kelts, and J. Southon. 1997b. Holocene paleohydrology of the tropical Andes from lake records. Quatern. Res. 47: 70–80.

———, B. B. Wolfe, R. Aravena, A. P. Wolfe, and G. O. Seltzer. 2000. Holocene hydrological reconstructions from stable isotopes and paleolimnology, Cordillera Real, Bolivia. Quatern. Sci. Rev. 19: 1801–1820.

Ab'Saber, A. N. 1978. A planície do tietê no Planalto Paulistano. Geomorfologia 57: 1–24.

———. 1982. The paleoclimate and paleoecology of Brazilian Amazonia. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 41–59.

Adams, C. G., D. E. Lee, and B. R. Rosen. 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 77: 289–313.

Aeschbach-Hertig, W., F. Peeters, U. Beyerle, and R. Kipfer. 2000. Palaeotemperature reconstruction from noble gases in ground water taking into account equilibration with entrapped air. Nature 405: 1040–1043.

Aguirre Urreta, M. B. 2002. Invertebrados del Cretácico Inferior. *In:* M. J. Haller (ed.), Geología y Recursos Naturales de Santa Cruz. Relatorio 15th Congreso Geológico Argentino (Calafate, Argentina, 2002): 439–459.

Alcalde, J. A. and J. J. Kulemeyer. 1999. The Holocene in the south-eastern region of the Province Jujuy, north-west Argentina. Quatern. Int. 57/58: 113–116.

Aldenderfer, M. 1999. The Pleistocene/Holocene transition in Peru and its effects upon human use of the landscape. Quatern. Int. 53/54: 11–19.

Ameghino, F. 1876. Ensayos de un estudio de los terrenos de transporte cuaternarios de la Provincia de Buenos Aires. *In:* Obras Completas y Correspondencia Científica de F. Ameghino, Vol. II, Primeros Trabajos Científicas. Gob. Prov. Buenos Aires 1914. La Plata, Argentina. pp. 55–137.

Andriessen, P. A. M., K. F. Helmens, H. Hooghiemstra, P. A. Riezebos, and T. van der Hammen. 1993. Absolute chronology of the Pliocene–Quaternary sediment sequence of the Bogotá area, Colombia. Quatern. Sci. Rev. 12: 483–501.

Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants; APG III. Bot. J. Linn. Soc. 161: 105–121.

Antoine, P.-O. et al. (+ 9 authors). 2006. Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. Proc. Natl. Acad. Sci. U.S.A. 103: 13,595–13,600.

Anzótegui, L. M. 1998. Hojas de angiospermas de la Formación Palo Pintado, Mioceno superior, Salta, Argentina. Parte I: Anacardiaceae, Lauraceae y Moraceae. Ameghiniana 35: 25–32.

Araujo, A. G. M., W. A. Neves, L. B. Piló, and J. P. V. Atui. 2005. Holocene dryness and human occupation in Brazil during the "Archaic Gap." Quatern. Res. 64: 298–307.

Archangelsky, A., C. J. Phipps, T. N. Taylor, and E. L. Taylor. 1999. *Paleoazolla*, a new heterosporous fern from the Upper Cretaceous of Argentina. Amer. J. Bot. 86: 1200–1206.

———, R. R. Andreis, S. Archangelsky, and A. Artabe. 1995. Cuticular characters adapted to volcanic stress in a new Cretaceous cycad leaf from Patagonia, Argentina. Considerations on the stratigraphy and depositional history of the Baqueró Formation. Rev. Palaeobot. Palynol. 89: 213–233.

Archangelsky, S. 1963a. Notas sobre la flora fósil de la zona de Ticó, Provincia de Santa Cruz. Ameghiniana 3: 57–62.

———. 1963b. Notas sobre la flora fósil de la zona de Ticó, Provincia de Santa Cruz. Tres nuevas especies de *Mesosingeria*. Ameghiniana 3: 113–120.

———. 1963c. Notas sobre la flora fósil de la zona de Ticó, Provincia de Santa Cruz. *Ruflorinia pilifera* n. sp., *Equisetites*. Ameghiniana 3: 221–226.

———. 1964. Notas sobre la flora de la zona de Ticó, Provincia de Santa Cruz. 5. *Sphenopteris* cf. *goepperti* Dunker. 6. *Cladophlebis* sp. Ameghiniana 3: 280–284.

———. 1968. On the genus *Tomaxellia* (Coniferae) from the Lower Cretaceous of Patagonia (Argentina) and its male and female cones. J. Linn. Soc. (Bot.) 61: 153–165.

———. 1970. Evolución de los estudios paleobotánicos en Argentina desde sus origenes hasta nuestros dias. Bol. Acad. Nac. Ci. 48: 551–557.

———. 1972. Esporas de la Formación Río Turbio (Eoceno), Provincia de Santa Cruz. Revista Mus. La Plata, Secc. Paleontol. 6(39): 65–100.

———. 1973. Palinología del Paleoceno de Chubut. 1. Descripciones sistemáticas. Ameghiniana 10: 339–399.

———. 1974. Sobre la edad de la tafoflora de La Laguna del

Hunco, Provincia de Chubut. Ameghiniana 11: 413–417.
———. 1988. *Gamerroites*, nuevo genero de polen bisacado del Cretácico de Patagonia, Argentina. Bol. Asoc. Latinoamer. Paleobot. Palin. 11: 1–6.
———. 1994. Comparative ultrastructure of three Early Cretaceous gymnosperm pollen grains: *Araucariacites*, *Balmeiopsis* and *Callialasporites*. Rev. Palaeobot. Palynol. 83: 185–198.
———. 2001. Evidences of an Early Cretaceous floristic change in Patagonia, Argentina. Asoc. Paleontol. Argentina, Publ. Especial 7: 15–19.
———. 2003. Flora Cretácica del Grupo Baqueró, Santa Cruz, Argentina. Monografías del Museo Argentino de Ciencias Naturales 4 [CD-ROM].
———. 2005. La paleobotánica en Argentina y su desarrollo durante los últimos 50 años. Asoc. Paleontol. Argentina, 50 Aniversario Publ. Especial 10: 37–49.
——— and A. Archangelsky. 2002. Palinología estadística en el Cretácico de la Cuenca Austral, plataforma continental Argentina. I. Seis perforaciones del área Magallanes. Revista Mus. Argent. Ci. Nat., n.s., 4: 25–34.
——— and ———. 2004. Palinología estadística en el Cretácico de la Cuenca Austral, platforma continental Argentina. II. Seis perforaciones del área Gallegos. III. Discusión y conclusiones. Revista Mus. Argent. Ci. Nat., n.s., 6: 245–255.
———, A. Baldoni, J. C. Gamerro, and J. Seiler. 1983. Palinología estratigráfica del Cretácico de Argentina austral, II. Descripciones sistemáticas. Ameghiniana 20: 199–226.
———, ———, ———, and ———. 1984. Palinología estratigráfica del Cretácico de Argentina austral. III. Distribución de las especies y conclusiones. Ameghiniana 21: 15–33.
———, E. S. Bellosi, G. A. Jalfin, and C. Perrot. 1994. Palynology and alluvial facies from the mid-Cretaceous of Patagonia, subsurface of San Jorge Basin, Argentina. Cretaceous Res. 15: 127–142.
——— and G. del Fueyo. 1987. Sobre una podocarpacea fertile del Cretácico Inferior de la Provincia Santa Cruz, República Argentina. Actas VII Simposio Argentino Paleobotánica Palinología (Buenos Aires): 85–87.
——— and ———. 1989. *Squamastrobus* Gen. N., a fertile podocarp from the Early Cretaceous of Patagonia, Argentina. Rev. Palaeobot. Palynol. 59: 109–126.
——— and J. C. Gamerro. 1965 et seq. Estudio palinológico de la Formación Baqueró (Cretácico), Provincia de Santa Cruz. I. Ameghiniana 4: 159–167.
———, L. Lezama, and A. Archangelsky. 2000. Bibliografía paleobotánica Argentina. Pub. Especial MEF (Museo Paleontológico Egidio Feruglio) No. 1: 1–83.
——— and E. J. Romero. 1974. Polen de gimnospermas (Coniferas) del Cretácico Superior y Paleoceno de Patagonia. Ameghiniana 11: 217–236.
——— and T. N. Taylor. 1986. Ultrastructural studies of fossil plant cuticles. II. *Tarphyderma* Gen. N., a Cretaceous conifer from Argentina. Amer. J. Bot. 73: 1577–1587.
——— and ———. 1993. The ultrastructure of in situ *Clavatipollenites* pollen from the Early Cretaceous of Patagonia. Amer. J. Bot. 80: 879–885.
——— and L. Villar de Seoane. 2004. Cycadean diversity in the Cretaceous of Patagonia, Argentina. Three new *Androstrobus* species from the Baqueró Group. Rev. Palaeobot. Palynol. 131: 1–28.
——— and ———. 2005. Estudios palinológicos del Grupo Baqueró (Cretácico Inferior), Provincia de Santa Cruz, Argentina. IX. Polen bisacado de Podocarpaceae. Revista Esp. Paleontol. 20: 37–56.
——— and M. del Carmen Zamaloa. 1986. Nuevas descripciones palinológicas de las formaciónes Salamanca y Bororo, Paleoceno de Chubut (República Argentina). Ameghiniana 23: 35–46.
Argollo, J. and P. Mourguiart. 2000. Late Quaternary climate history of the Bolivian Altiplano. Quatern. Int. 72: 37–51.
Artabe, A. E., A. B. Zamuner, and D. W. Stevenson. 2004. Two new petrified cycad stems, *Brunoa* gen. nov. and *Worsdellia* gen. nov., from the Cretaceous of Patagonia (Bajo de Santa Rosa, Río Negro Province), Argentina. Bot. Rev. 70: 121–133.
Arz, H. W., J. Pätzold, and G. Wefer. 1998. Correlated millennial-scale changes in surface hydrography and terrigenous sediment yield inferred from Last-glacial marine deposits off northeastern Brazil. Quatern. Res. 50: 157–166.
Askin, R. A. and S. R. Jacobson. 1996. Palynological change across the Cretaceous–Tertiary boundary on Seymour Island, Antarctica. *In:* N. MacLeod and G. Keller (eds.), Cretaceous–Tertiary Mass Extinctions: Biotic and Environmental Changes. Norton, New York. pp. 7–26.
Auler, A. S. et al. (+ 6 authors). 2004. Quaternary ecological and geomorphic changes associated with rainfall events in presently semiarid northeastern Brazil. J. Quatern. Sci. 19: 693–701.
Baker, P. A. et al. (+ 6 authors). 2001a. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. Nature 409: 698–701.
——— et al. (+ 8 authors). 2001b. The history of South American tropical precipitation for the past 25,000 years. Science 291: 640–643.
Baldoni, A. M. and S. Archangelsky. 1983. Palinología de la Formación Springhill (Cretácico Inferior), subsuelo de Argentina y Chile Austral. Rev. Esp. Micropaleontol. 15: 47–101.
——— and T. N. Taylor. 1983. Plant remains from a new Cretaceous site in Santa Cruz, Argentina. Rev. Palaeobot. Palynol. 39: 301–311.
Barberi, M., M. L. Salgado-Labouriau, and K. Suguio. 2000. Paleovegetation and paleoclimate of "Vereda de Águas Emendadas," central Brazil. J. S. Amer. Earth Sci. 13: 241–254.
Bard, E., F. Rostek, and C. Sonzogni. 1997. Interhemispheric

synchrony of the last deglaciation inferred from alkenone palaeothermometry. Nature 385: 707–710.

Barreda, V. D. 1996. Bioestratigrafía polen y esporas de la Formación Chenque, Oligoceno tardío?–Mioceno de las provincias de Chubut y Santa Cruz, Patagonia, Argentina. Ameghiniana 33: 35–56.

———. 1997a. Palinoestratigrafía de la Formación San Julián en el área de Playa La Mina (Provincia de Santa Cruz), Oligoceno de la cuenca austral. Ameghiniana 34: 283–294.

———. 1997b. Palynomorph assemblage of the Chenque Formation, late Oligocene?–Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Part 1: Terrestrial algae, trilete and monolete spores. Ameghiniana 34: 69–80.

———. 1997c. Palynomorph assemblage of the Chenque Formation, late Oligocene?–Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Part 2: Gymnosperm and colpate pollen. Ameghiniana 34: 81–92.

———. 1997d. Palynomorph assemblage of the Chenque Formation, late Oligocene?–Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Part 3: Polycolpate and tricolporate pollen. Ameghiniana 34: 131–144.

———. 1997e. Palynomorph assemblage of the Chenque Formation, late Oligocene?–Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Part 4: Polycolporate and porate pollen. Ameghiniana 34: 145–154.

———. 2007. Patagonian vegetation turnovers during the Paleogene–early Neogene: Origin of arid-adapted floras. Bot. Rev. 73: 31–50.

——— and E. Bellosi. 2003. Ecosistémas terrestres del Mioceno temprano de la Patagonia central, Argentina: Primeros avances. Revista Mus. Argent. Ci. Nat., n.s., 5: 125–134. [See also other papers in this volume from the XII Simposio Argentino de Paleobotánica y Palinología, Buenos Aires (April 2003).]

——— and M. Caccavari. 1992. Mimosoideae (Leguminosae) occurrences in the early Miocene of Patagonia (Argentina). Palaeogeogr. Palaeoclimatol. Palaeoecol. 94: 243–252.

———, P. R. Gutiérrez, and C. O. Limarino. 1998. Edad y paleoambiente de la "Serie del Yeso," Valle del Cura, Provincia de San Juan: Evidencias palinológicas. Ameghiniana 35: 321–335.

——— and S. Palamarczuk. 2000a. Palinoestratigrafía de depósitos del Oligoceno tardío–Mioceno en el área sur del Golfo Jorge, provincial de Santa Cruz, Argentina. Ameghiniana 37: 103–117.

——— and ———. 2000b. Estudio palinoestratigrafíco del Oligoceno tardío–Mioceno en secciones de la costa Patagónica y plataforma continental Argentina. *In:* F. G. Aceñolaza and R. Herbst (eds.), El Neógeno de Argentina. INSUGEO, Serie Correlación Geológica 14, Tucumán, Argentina. pp. 103–138.

——— and ———. 2000c. Palinomorfos continentales y marinos de la Formación Monte León en su área tipo, provincia de Santa Cruz, Argentina. Ameghiniana 37: 3–12.

———, ———, and J. A. Chamberlain Jr. 2004. Vegetational disruption at the Cretaceous/Paleogene boundary in Neuquén, Argentina: Evidence from spores and pollen. Abstract, 10th Reunión Argentina Sedimentologia (San Luis, Argentina, 2004): 185–186.

——— and L. Palazzesi. 2005. Patagonian vegetation turnovers during the Paleogene–early Neogene: Origin of arid-adapted floras. Abstract, XVI Congreso Geólogico Argentino (La Plata, November, 2005): 1 p.

Becker, L. 2002. Repeated blows. Sci. Amer. (March, 2002): 77–83.

Beehler, B. M., T. C. Stevenson, and M. Brown. 2004. Letters: Virgin rainforests and conservation. Science 305: 943–944.

Beheregaray, L. B. et al. (+ 5 authors). 2003. Genes record a prehistoric volcano eruption in the Galápagos. Science 302: 75.

Behling, H. 1995. Investigations into the late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). Veg. Hist. & Archaeobot. 4: 127–152.

———. 1996. First report on new evidence for the occurrence of *Podocarpus* and possible human presence at the mouth of the Amazon during the Late Glacial. Veg. Hist. & Archaeobot. 5: 241–246.

———. 1997a. Late Quaternary vegetation, climate and fire history of the *Araucaria* forest and campos region from Serra Campos Gerais, Paraná state (south Brazil). Rev. Palaeobot. Palynol. 97: 109–121.

———. 1997b. Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 129: 407–422.

———. 1998. Late Quaternary vegetational and climatic changes in Brazil. Rev. Palaeobot. Palynol. 99: 143–156.

———. 2002a. Late Quaternary vegetation and climate dynamics in southeastern Amazonia inferred from Lagoa da Confusão in Tocantins state, northern Brazil. Amazonia 17: 27–39.

———. 2002b. South and southeast Brazilian grasslands during late Quaternary times: A synthesis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 177: 19–27.

———, H. W. Arz, J. Pätzold, and G. Wefer. 2000. Late Quaternary vegetational and climatic dynamics in northeastern Brazil, inferences from marine core GeoB 3104–1. Quatern. Sci. Rev. 19: 981–994.

———, J. C. Berrio, and H. Hooghiemstra. 1999. Late Quaternary pollen records from the middle Caquetá River Basin in central Colombian Amazon. Palaeogeogr. Palaeoclimatol. Palaeoecol. 145: 193–213.

——— and H. Hooghiemstra. 1998a. Late Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of Los Llanos Orientales in Colombia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 139: 251–267.

——— and ———. 1998b. Holocene history of the chocó

rain forest from Laguna Piusbi, southern Pacific lowlands of Colombia. Quatern. Res. 50: 300–308.
——— and ———. 1999. Environmental history of the Colombian savannas of Los Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. J. Paleolimnol. 21: 461–476.
——— and ———. 2000. Holocene Amazon rainforest–savanna dynamics and climatic implications: High-resolution pollen record from Laguna Loma Linda in eastern Colombia. J. Quatern. Sci. 15: 687–695.
——— and ———. 2001. Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 307–323.
——— and M. Lichte. 1997. Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. Quatern. Res. 48: 348–358.
——— and M. Lima da Costa. 1994. Studies on Holocene tropical vegetation mangrove and coast environments in the state of Maranhão, NE Brazil. *In:* J. Rabassa and M. Salemme (eds.), Quaternary of South America and Antarctic Peninsula, Vol. 10. Balkema Publishers, Leiden. pp. 93–118.
——— and ———. 2000. Holocene environmental changes from the Rio Curuá record in the Caxiuanã region, eastern Amazon Basin. Quatern. Res. 53: 369–377.
———, V. DePatta Pillar, L. Orlóci, and S. Girardi Bauermann. 2004. Late Quaternary *Araucaria* forest, grassland (campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 203: 277–297.
Bennett, K. D., S. G. Haberle, and S. H. Lumley. 2000. The last glacial–Holocene transition in southern Chile. Science 290: 325–328.
Berrío, J. C., H. Hooghiemstra, H. Behling, and K. van der Borg. 2000. Late Holocene history of savanna gallery forest from Carimagua area, Colombia. Rev. Palaeobot. Palynol. 111: 295–308.
Berry, E. W. 1917. Fossil plants from Bolivia and their bearing on the age of uplift of the Eastern Andes. Proc. U. S. Natl. Mus. 54: 103–164.
———. 1919. Miocene fossil plants from northern Peru. Proc. U. S. Natl. Mus. 55: 279–294.
———. 1922a. Contributions to the paleobotany of Peru, Bolivia and Chile. Johns Hopkins Univ. Stud. Geol. 4: 1–221.
———. 1922b. Pliocene fossil plants from eastern Bolivia. Johns Hopkins Univ. Stud. Geol. 4: 145–204.
———. 1922c. Tertiary fossil plants from Venezuela. Proc. U. S. Natl. Mus. 59: 553–579.
———. 1922d. Late Tertiary plants from Jancocata, Bolivia. Johns Hopkins Univ. Stud. Geol. 4: 205–220.
———. 1924a. Mesozoic plants from Patagonia. Amer. J. Sci. 7: 473–482.
———. 1924b. New Tertiary species of *Anacardium* and *Vantanea* from Colombia. Pan-Amer. Geol. 42: 259–262.
———. 1924c. A fossil *Celtis* from Colombia. Torreya 24: 44–46.
———. 1924–25. Fossil fruits from the Eastern Andes of Colombia. Bull. Torrey Bot. Club 51: 61–67.
———. 1925a. A banana in the Tertiary of Colombia. Amer. J. Sci. 10: 530–537.
———. 1925b. A Miocene flora from Patagonia. Johns Hopkins Univ. Stud. Geol. 6: 183–251.
———. 1925c. Tertiary plants from eastern Peru. Johns Hopkins Univ. Stud. Geol. 6: 163–182.
———. 1925d. The Tertiary flora of the Island of Trinidad, B.W.I. Johns Hopkins Univ. Stud. Geol. 6: 71–162.
———. 1925e. A Pleistocene flora from the island of Trinidad. Proc. U. S. Natl. Mus. 66: 1–9.
———. 1925f. Miocene Araceae related to *Caladium* from Trinidad. Pan-Amer. Geol. 44: 38–42.
———. 1927. Petrified fruits and seeds from Oligocene of Peru. Pan-Amer. Geol. 47: 121–132.
———. 1929a. Tertiary fruits and seeds from northwestern Peru. Johns Hopkins Univ. Stud. Geol. 10: 137–180.
———. 1929b. Eocene plants from Restin Formation of Peru. Pan-Amer. Geol. 51: 241–244.
———. 1929c. Fossil fruits in the Ancón Sandstone of Ecuador. J. Paleontol. 3: 298–301.
———. 1929d. The fossil flora of the Loja Basin in southern Ecuador. Johns Hopkins Univ. Stud. Geol. 10: 79–136.
———. 1933. A *Jacaranda* from the Pliocene of Brazil. Torreya 33: 38–40.
———. 1936a. Tertiary plants from Venezuela. Proc. U. S. Natl. Mus. 83: 335–360.
———. 1936b. Miocene plants from Colombia, South America. Bull. Torrey Bot. Club 63: 53–66.
———. 1936c. Tertiary plants from Brazil. Proc. Amer. Philos. Soc. 75: 565–590.
———. 1937a. An Upper Cretaceous flora from Patagonia. Contributions to Paleobotany of South America. Johns Hopkins Univ. Stud. Geol. 12: 11–31.
———. 1937b. A Paleocene flora from Patagonia. Contributions to Paleobotany of South America. Johns Hopkins Univ. Stud. Geol. 12: 33–50.
———. 1937c. Eocene plants from Río Turbio in the territory of Santa Cruz, Patagonia. Contributions to Paleobotany of South America. Johns Hopkins Univ. Stud. Geol. 12: 91–97.
———. 1937d. On the presence of the fern *Weichselia* in Colombia, South America. J. Wash. Acad. Sci. 27: 458–461.
———. 1937e. *Gyrocarpus* and other fossil plants from the Cumarebo field in Venezuela. J. Wash. Acad. Sci. 27: 501–506.
———. 1937f. Late Tertiary plants from the Territory of Acre, Brazil. Johns Hopkins Univ. Stud. Geol. 12: 81–90.

———. 1937g. A flora from the forest clay of Trinidad. Contributions to the Paleobotany of South America. Johns Hopkins Univ. Stud. Geol. 12: 51–68.

———. 1937h. A Late Tertiary flora from Trinidad. Johns Hopkins Univ. Stud. Geol. 12: 69–79.

———. 1938. Tertiary flora from the Río Pichileufu, Argentina. Geol. Soc. Amer. Spec. Paper 12: 1–149.

———. 1939a. Eocene plants from a well core in Venezuela. Johns Hopkins Univ. Stud. Geol. 13: 157–161.

———. 1939b. The fossil flora of Potosí, Bolivia. Johns Hopkins Univ. Stud. Geol. 13: 9–67.

———. 1939c. Fossil plants from the state of Anzoategui, Venezuela. Johns Hopkins Univ. Stud. Geol. 13: 137–155.

———. 1940. A *Cusparia* from the Pliocene of trans-Andean Bolivia. J. Wash. Acad. Sci. 30: 464–467.

———. 1945a. Fossil floras from southern Ecuador. Johns Hopkins Univ. Stud. Geol. 14: 93–150.

———. 1945b. Late Tertiary fossil plants from eastern Colombia. Johns Hopkins Univ. Stud. Geol. 14: 171–186.

Bertaux, J. et al. (+ 7 authors). 2002. Paleoclimatic record of speleothems in a tropical region: Study of laminated sequences from a Holocene stalagmite in central-west Brazil. Quatern. Int. 89: 3–16.

Betancourt, J. L. 2004. Arid lands paleobiogeography: The rodent midden record in the Americas. *In:* M. V. Lomolino and L. R. Heaney (eds.), Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland, MA. pp. 27–46.

———, C. Latorre, J. A. Rech, J. Quade, and K. A. Rylander. 2000. A 22,000-year record of monsoonal precipitation from northern Chile's Atacama Desert. Science 289: 1542–1546.

Bigarella, J. J. 1971. Variações climáticas no Quaternário superior do Brasil e sua datação radiométrica pelo método do carbono 14. Paleoclimas 1: 1–22.

Blunier, T. et al. (+ 10 authors). 1998. Asynchrony of Antarctic and Greenland climate change during the last glacial period. Nature 394: 739–743.

Boom, A., R. Marchant, H. Hooghiemstra, and J. S. Sinninghe Damsté. 2002. CO_2- and temperature-controlled altitudinal shifts of C_4- and C_3-dominated grasslands allow reconstruction of palaeoatmospheric pCO_2. Palaeogeogr. Palaeoclimatol. Palaeoecol. 177: 151–168.

———, G. Mora, A. M. Cleef, and H. Hooghiemstra. 2001. High altitude C_4 grasslands in the Northern Andes: Relicts from glacial conditions? Rev. Palaeobot. Palynol. 115: 147–160.

Bradbury, J. P. et al. (+ 8 authors). 1981. Late Quaternary environmental history of Lake Valencia, Venezuela. Science 214: 1299–1305.

Brinkhuis, H. et al. (+ 21 authors and the Expedition 302 Scientists). 2006. Episodic fresh surface waters in the Eocene Arctic Ocean. Nature 441: 606–609.

Britton, N. L. 1892. Note on a collection of Tertiary fossil plants from Potosí, Bolivia. Trans. Amer. Inst. Mining Engin. 21: 250–259.

Brown, K. S., Jr., P. M. Sheppard, and J. R. G. Turner. 1974. Quaternary refugia in tropical America: Evidence from race formation in *Heliconius* butterflies. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 187: 369–378.

Brown, R. W. 1934. The supposed fossil ear of maize from Cuzco, Peru. J. Wash. Acad. Sci. 24: 293–296.

———. 1946. Walnuts from the Late Tertiary of Ecuador. Amer. J. Sci. 244: 554–556.

Burbridge, R. E., F. E. Mayle, and T. J. Killeen. 2004. Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. Quatern. Res. 61: 215–230.

Burnham, R. J. 1994. Patterns in tropical leaf litter and implications for angiosperm paleobotany. Rev. Palaeobot. Palynol. 81: 99–113.

———. 1995. A new species of winged fruit from the Miocene of Ecuador: *Tipuana ecuatoriana* (Leguminosae). Amer. J. Bot. 82: 1599–1607.

——— and N. L. Carranco. 2004. Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes. Amer. J. Bot. 91: 1767–1773.

Bush, M. B., P. A. Colinvaux, M C. Wiemann, D. R. Piperno, and K.-b. Liu. 1990. Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. Quatern. Res. 34: 330–345.

——— et al. (+ 8 authors). 2005. A 17,000-year history of Andean climate and vegetation change from Laguna de Chochos, Peru. J. Quatern. Sci. 20: 703–714.

———, M. R. Silman, and D. U. Urrego. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. Science 303: 827–829.

Caccavari, M. and V. Barreda. 2000. A new calymmate mimosoid polyad from the Miocene of Argentina. Rev. Palaeobot. Palynol. 109: 197–203.

Campbell, K. E., Jr., C. D. Frailey, and L. Romero-Pittman. 2006. The pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239: 166–219.

Cantrill, D. J. and N. S. Nagalingum. 2005. Ferns from the Cretaceous of Alexander Island, Antarctica: Implications for Cretaceous phytogeography of the Southern Hemisphere. Rev. Palaeobot. Palynol. 137: 83–103.

Carignano, C. A. 1999. Late Pleistocene to recent climate change in Córdoba Province, Argentina: Geomorphological evidence. Quatern. Int. 57/58: 117–134.

Chepstow-Lusty, A. et al. (+ 5 authors). 2005. Vegetation and climate change on the Bolivian Altiplano between 108,000 and 18,000 yr ago. Quatern. Res. 63: 90–98.

Christie, D. M. et al. (+ 6 authors). 1992. Drowned islands downstream from the Galapagos hotspot imply extended speciation times. Nature 355: 246–248.

Cioccale, M. A. 1999. Climatic fluctuations in the central region of Argentina in the last 1000 years. Quatern. Int. 62:

35–47.
Cladera, G., R. Andreis, S. Archangelsky, and R. Cúneo. 2002. Estratigrafía del Grupo Baqueró, Patagonia (Provincia de Santa Cruz, Argentina). Ameghiniana 39: 3–20.
Clapperton, C. M. 1979. Glaciation in Bolivia before 3.27 Myr. Nature 277: 375–377.
———. 1993. Quaternary Geology and Geomorphology of South America. Elsevier Science Publishers, Amsterdam.
———, J. D. Clayton, D. I. Benn, C. J. Marden, and J. Argollo. 1997. Late Quaternary glacier advances and palaeolake highstands in the Bolivian Altiplano. Quatern. Int. 38/39: 49–59.
CLIMAP Project Members. 1976. The surface of the ice-age Earth. Science 191: 1131–1137.
———. 1981. Seasonal Reconstruction of the Earth's Surface at the Last Glacial Maximum. Map Chart Series MC-36. Geological Society of America, Boulder, CO.
———. 1984. The last interglacial ocean. Quatern. Res. 21: 123–224.
Cohen, M. C. L., H. Behling, and R. J. Lara. 2005. Amazonian mangrove dynamics during the last millennium: The relative sea-level and the Little Ice Age. Rev. Palaeobot. Palynol. 136: 93–108.
COHMAP Members. 1988. Climatic changes of the last 18,000 years: Observations and model simulations. Science 241: 1043–1052.
Coimbra, A. M., C. Riccomini, and M. S. Melo. 1983. A formação Itaquaquecetuba: Evidências de tectonismo no Quaternário Paluista. Atlas 4º Simpósio Regional Geología (São Paulo, 1983): 253–266.
Colinvaux, P. A. and E. K. Schofield. 1976a. Historical ecology in the Galápagos Islands. I. Holocene pollen record from El Junco Lake, Isla San Cristobal. J. Ecol. 64: 989–1012.
——— and ———. 1976b. Historical ecology in the Galápagos Islands. II. A Holocene spore record from El Junco Lake, Isla San Cristobal. J. Ecol. 64: 1013–1026.
Collins, G. N. 1919. A fossil ear of maize. J. Heredity 10: 170–172.
———. 1923. An ear of prehistoric maize that resembles the fossil form, *Zea antiqua*. J. Heredity 14: 61–64.
Collinson, M. E., M. C. Boulter, and P. L. Holmes. 1993. Magnoliophyta ("Angiospermae"). The Fossil Record 2. Chapman & Hall, London.
Colmenares C., O. A. 1988. A palynological study of samples from three wells of the Boscan Field, Venezuela. Revista Técnica Intevep 8: 83–97.
Cookson, I. C. and L. M. Cranwell. 1967. Lower Tertiary microplankton, spores and pollen grains from southernmost Chile. Micropaleontology 13: 204–216.
——— and K. M. Pike. 1954. Some dicotyledonous pollen types from Cainozoic deposits in Australian region. Australian J. Bot. 2: 197–219.
Coronato, A., M. Salemme, and J. Rabassa. 1999. Palaeoenvironmental conditions during the early peopling of southernmost South America (Late Glacial–early Holocene, 14–8 ka B.P.). Quatern. Int. 53/54: 77–92.
Couper, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geol. Surv. Paleontol. Bull. 22: 1–77.
———. 1960. New Zealand Mesozoic and Cainozoic plant microfossils. New Zealand Geol. Surv. Paleontol. Bull. 32: 1–87.
Crawford, D. J. 2006. What molecules do (and don't) say about angiosperm evolution. Trends Ecol. Evol. 21: 237. [Review of *Phylogeny and Evolution of Angiosperms*, Soltis et al., 2005.]
Cruz, F. W., Jr. et al. (+ 8 authors). 2005. Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. Nature 434: 63–66.
Cunéo, R. and M. A. Gandolfo. 2005. Angiosperm leaves from the Kachaike Formation, Lower Cretaceous of Patagonia, Argentina. Rev. Palaeobot. Palynol. 136: 29–47.
Curry, W. B. and D. W. Oppo. 1997. Synchronous, high-frequency oscillations in tropical sea surface temperatures and North Atlantic deep water production during the last glacial cycle. Paleooceanography 12: 1–14.
Da Silva, M. N. F. and J. L. Patton. 1993. Amazonian phylogeography: mtDNA sequence variation in arboreal echimyid rodents (Caviomorpha). Molec. Phylogen. Evol. 2: 243–255.
Delevoryas, T. and S. C. Srivastava. 1981. Jurassic plants from the department of Francisco Morazán, central Honduras. Rev. Palaeobot. Palynol. 34: 345–357.
Del Fueyo, G. M. and S. Archangelsky. 2001. New studies on *Karkenia incurva* Archang. from the Early Cretaceous of Argentina. Evolution of the seed cone in Ginkgoales. Palaeontographica, Abt. B, Paläophytol. 256: 111–121.
——— and ———. 2005. A new Araucarian pollen cone with in situ *Cyclusphaera* Elsik from the Aptian of Patagonia, Argentina. Cretaceous Res. 26: 757–768.
De Lima, M. R. 1978. Palinologia da Formacão Santana (Cretáceo do nordeste do Brasil). Introducão geológica e descricão sistemática dos esporos da Subturma Azonotriletes. Ameghiniana 15: 333–365.
———. 1979. Palinologia da Formacão Santana (Cretáceo do nordeste do Brasil). II. Descricão sistemática dos esporos da Subturma Zonotriletes e Turma Monoletes, e dos polens das Turma Saccites e Aletes. Ameghiniana 16: 27–63.
———. 1980. Palinologia da Formacão Santana (Cretáceo do nordeste do Brasil). III. Descricão sistemática dos polens da Turma Plicates (Subturma Costates). Ameghiniana 17: 15–47.
———. 1982. Palinología da Formação Codô, Maranhão. Bol. Inst. Geoci. Univ. São Paulo 13: 43–134.
———. 1989. Palinologia da Formacão Santana (Cretáceo do nordeste do Brasil). IV. Descricão sistemática dos polens das Turmas Plicates e Poroses, esporos, Incertae Sedis e

microplancton marinho. Ameghiniana 26: 63–81.

del Papa, C., V. García, and M. Quattrocchio. 2002. Sedimentary facies and paleofacies assemblages in an Eocene perennial lake, Lumbrera Formation, northwest Argentina. J. S. Amer. Earth Sci. 15: 553–569.

De Oliveira, P. E., A. M. Franca Barreto, and K. Suguio. 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: The fossil dunes of the middle São Francisco River. Palaeogeogr. Palaeoclimatol. Palaeoecol. 152: 319–337.

Dettinger, M. D., D. S. Battisti, R. D. Garreaud, G. J. McCabe Jr., and C. M. Bitz. 2001. Interhemispheric effects of interannual and decadal ENSO-like climate variations on the Americas. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 1–16.

Dettmann, M. E. 1986. Significance of the Cretaceous–Tertiary spore genus *Cyatheacidites* in tracing the origin and migration of *Lophosoria* (Filicopsida). Special Pap. Paleontol. 35: 63–94.

——— and H. T. Clifford. 1992. Phylogeny and biogeography of *Ruffordia*, *Mohria*, and *Anemia* (Schizaeaceae) and *Ceratopteris* (Pteridaceae): Evidence from in situ and dispersed spores. Alcheringa 16: 269–314.

———, D. T. Pocknall, E. J. Romero, and M. del C. Zamaloa. 1990. *Nothofagidites* Erdtman ex Potonié, 1960: A catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (southern beech). New Zealand Geol. Surv. Palaeontol. Bull. 60: 1–79.

Díaz de Gamero, M. L. 1996. The changing course of the Orinoco River during the Neogene: A review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 123: 385–402.

Di Giacomo, E. de. 1985. *Orchidamasulitis schlechteri* nov. gen. et sp.—Fósil de orchídea (masula) de edad Oligoceno encontrada en Venezuela. Proc. VI Congr. Geol. Venezuela 1: 530–535.

——— and A. W. van Erve. 1987. *Janmulleripollis*, a new pollen genus from the Eocene of Venezuela. Contr. Ser. Amer. Assoc. Stratigr. Palynologists 19: 1–5.

Dilcher, D. L., M. E. Bernardes-de-Oliveira, D. Pons, and T. A. Lott. 2005. Welwitschiaceae from the Lower Cretaceous of northeastern Brazil. Amer. J. Bot. 92: 1294–1310.

DiMichele, W. A. et al. (+ 6 authors). 2004. Long-term stasis in ecological assemblages: Evidence from the fossil record. Ann. Rev. Ecol. Evol. Syst. 35: 285–322.

Dolianiti, E. 1955. Frutos de *Nipa* no Paleoceno de Pernambuco, Brasil. Divisão Geol. Mineral. Bol. 158: 1–36.

Doubinger, J. 1976. Quelques associations sporo-polliniques du Tertiaire de Colombie. Actes 97e Congrès Nat. Soc. Savantes (Nantes, 1972) 4: 9–18.

——— and P. Chotin. 1975. Etude palynologique de lignites Tertiaries du Basin d'Arauco–Concepcion (Chile). Rev. Esp. Micropaleontol. 7: 549–565.

——— and D. Pons. 1971. Les champignons épiphylles du Tertiaire de Colombie. I. Le gisement de Cerrejón (Paléocène–Éocène). Actes 96e Congrès Nat. Soc. Savantes (Toulouse, 1971) 5: 233–252.

——— and ———. 1975. Les champignons épiphylles de la Formation Guaduas (Maastrichtian, Bassin de Boyaca, Colombie). Actes 95e Congrès Nat. Soc. Savantes (Reims, 1970) 3: 145–162.

Duarte, L. 1956. Melastomataceae fósseis da bacia Terciária de Fonseca, Minas Gerais. Serv. Grãfico Inst. Brasil. Geogr. Estatística Bol. No. 161: 7–28.

———. 1958. Annonaceae fósseis da bacia Terciária de Fonseca, Minas Gerais. Serviço Grãfico Inst. Brasil. Geogr. Estatística Bol. No. 178: 7–27.

———. 1959. Styracaceae fóssil do Pleistoceno de Russas, Ceará. Notas Preliminares e Estudios, Dept. Nac. Produção Mineral (Rio de Janeiro) 109: 1–15.

———. 1970. Comentários sôbre o "status" taxinômico de uma colção de vegetais fosseis do Acre. Ann. Acad. Brasil. Sci. 42: 471–476.

Dueñas Jimenez, H. 1989. Asociaciones palinologicas de las formaciones Colón y Molino, nor-oriente Colombiano. Bol. Inst. Geoci. Univ. São Paulo, Publ. Espec. 7: 173–181.

Durango de Cabrera, J. and E. J. Romero. 1988. *Roupala patagonica* n. sp. (Proteaceae) del Paleocene de Chubut, República Argentina. Actas 3, IV Congr. Argent. Paleontol. y Bioestratigrafía (Mendoza, 1986): 121–124.

Edgar, K. M., P. A. Wilson, P. F. Sexton, and Y. Suganuma. 2007. No extreme bipolar glaciation during the main Eocene calcite compensation shift. Nature 448: 908–911.

Elsik, W. C. 1964. A new sporomorph genus from eastern Peru. Pollen & Spores 6: 601–604.

———. 1966. New sporomorph genera from the Upper Cretaceous of Peru. Pollen & Spores 8: 553–564.

Emiliani, C. 1955. Pleistocene temperatures. J. Geol. 63: 538–578.

Engelhardt, H. 1887. Ueber fossile Blattreste vom Cerro de Potosí in Bolivia. Sitzungsber. Abh. Naturwiss. Ges. Isis Dresden 5: 36–38.

———. 1891. Über Tertiärpflanzen von Chile. Abh. Senckenberg. Naturf. Ges. 16: 629–692.

———. 1894. Ueber neue fossile Pflanzenreste vom Cerro de Potosí. Sitzungsber. Abh. Naturwiss. Ges. Isis Dresden 1: 3–13.

———. 1895. Über neue Tertiärpflanzen Süd-Amerikas. Abh. Senckenberg. Naturf. Ges. 19: 1–47.

Fedorov, A. V. et al. (+ 7 authors). 2006. The Pliocene paradox (Mechanisms for a permanent El Niño). Science 312: 1485–1489.

Ferraz-Vicentini, K. R. and M. L. Salgado-Labouriau. 1996. Palynological analysis of a palm swamp in central Brazil. J. S. Amer. Earth Sci. 9: 207–219.

Feruglio, E. 1937. Una interesante Filicinea fósil de la Patagonia. Bol. Inform. Petrol. 14: 5–20.

Fittipaldi, F. C., M. Guímarães Simões, A. M. Giulietti, and J. Rubens Pirani. 1989. Fossil plants from the Itaquaquecetuba Formation (Cenozoic of the São Paulo Basin) and

their possible paleoclimatic significance. Bol. Inst. Geoci. Univ. São Paulo, Publ. Espec. 7: 183–203.

Forest, C. E., P. Molnar, and K. A. Emanuel. 1995. Palaeoaltimetry from energy conservation principles. Nature 374: 347–350.

———, J. A. Wolfe, P. Molnar, and K. A. Emanuel. 1998. Palaeoaltimetry incorporating atmospheric physics and botanical estimates of paleoclimate. Geol. Soc. Amer. Bull. 111: 497–511.

Freile, C. 1972. Estudio palinológico de la Formación Cerro Dorotea (Maastrichtiano–Paleoceno) de la Provincia de Santa Cruz. Revista Mus. La Plata, Secc. Paleontol. 6(38): 39–63, lamina II, Fig. 15.

Frenguelli, J. 1943a. Restos de *Casuarina* en el Mioceno de El Mirador, Patagonia Central. Notas Mus. La Plata, Paleontol. 8(56): 349–354.

———. 1943b. Proteáceas del Cenozoico de Patagonia. Notas Mus. La Plata 8: 201–213.

———. 1953a. Restos de género "*Eucalyptus*" en el Mioceno del Neuquén. Notas Mus., Univ. Nac. Eva Peron, Paleontol. 16: 209–213.

———. 1953b. La flora fósil de la región del alto Río Chalia en Santa Cruz (Patagonia). Notas Mus., Univ. Nac. Eva Peron, Paleontol. 16: 239–257.

———. 1957. El glaciarismo cuaternario. Sociedad Argentina de Estudios Geográficos (GAEA, Buenos Aires, Argentina) 11: 117–213.

Fritz, S. C. et al. (+ 9 authors). 2004. Hydrologic variation during the last 170,000 years in the Southern Hemisphere tropics of South America. Quatern. Res. 61: 95–104.

Fuenzalida V., H. 1964. Los afloramientos plantíferos de "El Arrayán," inmediaciones de Santiago. Noticiario Mensual, Museo Nacional de Historia Natural (Santiago, Chile) 100: 1–3.

Furness, C. A. and P. J. Rudall. 2004. Pollen aperture evolution—A crucial factor for eudicot success? Trends Pl. Sci. 9: 154–158.

Gamerro, J. C. 1968. Orbiculas (corpusculos de Ubisch) y membranas tapetales cutinizadas en cuatro coniferas del Cretácico Inferior de Santa Cruz, República Argentina. Ameghiniana 5: 271–278.

———. 1975. Megasporas del Cretácico de Patagonia. II. Megasporas petrificadas de la Formación La Amarga, Cretácico Inferior, Prov. Neuquén. Actas I Congreso Argentino de Paleontología y Bioestratigrafía (Tucumán, 1974) 2: 11–28.

———. 1977. Megasporas del Cretácico de Patagonia. III. Megasporas petrificadas del "Chubutense," Prov. del Chubut, Argentina. Ameghiniana 14: 100–116.

Gandolfo, M. A. and R. N. Cúneo. 2005. Fossil Nelumbonaceae from the La Colonia Formation (Campanian–Maastrichtian, Upper Cretaceous), Chubut, Patagonia, Argentina. Rev. Palaeobot. Palynol. 133: 169–178.

Garcia, A., M. Zárate, and M. M. Páez. 1999. The Pleistocene/Holocene transition and human occupation in the Central Andes of Argentina: Agua de la Cueva locality. Quatern. Int. 53/54: 43–52.

Garner, H. F. 1975. Radiometric evidence for pre-Wisconsin glaciation in the Northern Andes: Comment. Geology 3: 230–231.

Garreaud, R., M. Vuille, and A. C. Clement. 2003. The climate of the Altiplano: Observed current conditions and mechanisms of past changes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 5–22.

Gaupp, R., A. Kött, and G. Wörner. 1999. Palaeoclimatic implications of Mio–Pliocene sedimentation in the high-altitude intra-arc Lauca Basin of northern Chile. Palaeogeogr. Palaeoclimatol. Palaeoecol. 151: 79–100.

Genthon, C. et al. (+ 7 authors). 1987. Vostok ice core: Climatic response to CO_2 and orbital forcing changes over the last climatic cycle. Nature 329: 414–418.

Germeraad, J. H., C. A. Hopping, and J. Muller. 1968. Palynology of Tertiary sediments from tropical areas. Rev. Palaeobot. Palynol. 6: 189–348.

Gilli, A. et al. (+ 6 authors). 2001. Tracking abrupt climate change in the Southern Hemisphere: A seismic stratigraphic study of Lago Cardiel, Argentina (49°S). Terra Nova 13: 443–448.

Gómez, A., J. C. Berrío, H. Hooghiemstra, M. Becerra, and R. Marchant. 2007. A Holocene pollen record of vegetation change and human impact from Pantano de Vargas, an intra-Andean Basin of Duitama, Colombia. Rev. Palaeobot. Palynol. 145: 143–157.

González, C., L. E. Urrego, and J. I. Martínez. 2006. Late Quaternary vegetation and climate change in the Panama Basin: Palynological evidence from marine cores ODP 677B and TR 163–38. Palaeogeogr. Palaeoclimatol. Palaeoecol. 234: 62–80.

González-Guzmán, A. E. 1967. A Palynological Study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene; Tibú Area, Colombia). E. J. Brill, Leiden, The Netherlands.

González-Michaels, N., L. A. Forero Trujillo, and J. O. Rangel-Ch. 2002. Cambios en la vegetación y el clima durante el pleniglacial medio superior en el Valle de Tenjo (Cundinamarca, Colombia). Caldasia 24: 15–32.

Gosling, W. D., F. E. Mayle, N. J. Tate, and T. J. Killeen. 2005. Modern pollen-rain characteristics of tall *terra firme* moist evergreen forest, southern Amazonia. Quatern. Res. 64: 284–297.

Graf, K. 1981a. A Quaternary pollen profile from the upper valley of Cochabamba (Bolivia). *In:* E. B. Evenson, C. Schlüchter, and J. Rabassa (eds.), Tills and Related Deposits: Genesis, Petrology, Application, Stratigraphy. A. A. Balkema, Rotterdam, The Netherlands. pp. 365–372.

———. 1981b. Palynological investigations of two post-glacial peat bogs near the boundary of Bolivia and Peru. J. Biogeogr. 8: 353–368.

Graham, A. 1988. Studies in Neotropical paleobotany. VI. The lower Miocene communities of Panama—The Cucaracha Formation. Ann. Missouri Bot. Gard. 75: 1467–1479.

———. 1994. Neotropical Eocene coastal floras and $^{18}O/^{16}O$-estimated warmer vs. cooler equatorial waters. Amer. J. Bot. 81: 301–396.

———, K. M. Gregory-Wodzicki, and K. L. Wright. 2001. Studies in Neotropical paleobotany. XV. A Mio–Pliocene palynoflora from the Eastern Cordillera, Bolivia: Implications for the uplift history of the Central Andes. Amer. J. Bot. 88: 1545–1557.

Gregory-Wodzicki, K. M. 2000. Relationships between leaf morphology and climate, Bolivia: Implications for estimating paleoclimate from fossil floras. Paleobiology 26: 668–688.

———, W. C. McIntosh, and K. Velásquez. 1998. Climate and tectonic implications of the late Miocene Jakokkota flora, Bolivian Altiplano. J. S. Amer. Earth Sci. 11: 533–560.

Grimm, E., G. L. Jacobson Jr., W. A. Watts, B. C. S. Hansen, and K. A. Maasch. 1993. A 50,000-year record of climate oscillations from Florida and its temporal correlation with Heinrich events. Science 261: 198–200.

Grosjean, M. 1994. Paleohydrology of the Laguna Lejía (north Chilean Altiplano) and climatic implications for late-glacial times. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 89–100.

———, I. Cartajena, M. A. Geyh, and L. Núñez. 2003. From proxy data to paleoclimate interpretation: The mid-Holocene paradox of the Atacama Desert, northern Chile. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 247–258.

——— and L. Núñez A. 1994. Lateglacial, early and middle Holocene environments, human occupation, and resource use in the Atacama (northern Chile). Geoarcheology 9: 271–286.

———, ———, and I. Cartajena. 2005. Palaeoindian occupation of the Atacama Desert, northern Chile. J. Quatern. Sci. 20: 643–653.

——— et al. (+ 9 authors). 2001. A 22,000 ^{14}C year BP sediment and pollen record of climate change from Laguna Miscanti (23°S), northern Chile. Global Planet. Change 28: 35–51.

Guilderson, T. P., R. G. Fairbanks, and J. L. Rubenstone. 1994. Tropical temperature variations since 20,000 years ago: Modulating interhemispheric climate change. Science 263: 663–665.

Guler, M. V. and S. Archangelsky. 2002. Quistes de dinoflagelados de la Formación Kachaike (Cretácico Inferior), provincia de Santa Cruz, Argentina. Abstract, 8th Congreso Argentino Paleontología Bioestratigrafía (Corrientes, 2002): 71.

———, G. R. Guerstein, and M. E. Quattrocchio. 2001. Palinología del Neógeno de la Perforación Cx-1, Cuenca del Colorado, Argentina. Rev. Esp. Micropaleontol. 33: 183–204.

Haas, J. and M. O. Dillon (eds.). 2003. El Niño in Peru: Biology and culture over 10,000 years. Fieldiana, Bot., n.s. 43: 1–107.

Haberle, S. G. and M. A. Maslin. 1999. Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. Quatern. Res. 51: 27–38.

Hall, M. L. 1983. Origin of Española Island and the age of terrestrial life on the Galápagos Islands. Science 221: 545–547.

Halle, T. G. 1913. Some Mesozoic plant-bearing deposits in Patagonia and Tierra del Fuego and their floras. Kungl. Svenska Vetenskapsakad. Handl. 51: 1–58.

Hambler, C. 2004. Letters: Virgin rainforests and conservation. Science 305: 943–944.

Hanselman, J. A., W. D. Gosling, G. M. Paduano, and M. B. Bush. 2005. Contrasting pollen histories of MIS 5e and the Holocene from Lake Titicaca (Bolivia/Peru). J. Quatern. Sci. 20: 663–670.

Hansen, B. C. S. 1995. A review of lateglacial pollen records from Ecuador and Peru with reference to the Younger Dryas Event. Quatern. Sci. Rev. 14: 853–865.

——— et al. (+ 5 authors). 2003. Late-glacial and Holocene vegetational history from two sites in the Western Cordillera of southwestern Ecuador. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 79–108.

———, G. O. Seltzer, and H. E. Wright Jr. 1994. Late Quaternary vegetational change in the central Peruvian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 263–285.

———, H. E. Wright Jr., and J. P. Bradbury. 1984. Pollen studies in the Junín area, central Peruvian Andes. Geol. Soc. Amer. Bull. 95: 1454–1465.

Harris, S. E. and A. C. Mix. 1999. Pleistocene precipitation balance in the Amazon Basin recorded in deep sea sediments. Quatern. Res. 51: 14–26.

Haug, G. H., K. A. Hughen, D. M. Sigman, L. C. Peterson, and U. Röhl. 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. Science 293: 1304–1308.

——— et al. (+ 5 authors). 2003. Climate and the collapse of Maya civilization. Science 299: 1731–1735.

Heine, K. 2000. Tropical South America during the Last Glacial Maximum: Evidence from glacial, periglacial and fluvial records. Quatern. Int. 72: 7–21.

——— and J. T. Heine. 1996. Late glacial climate fluctuations in Ecuador: Glacial retreat during Younger Dryas time. Arctic Alpine Res. 28: 496–501.

Helmens, K. F., P. Kuhry, N. W. Rutter, K. van der Borg, and A. F. M. De Jong. 1996. Warming at 18,000 yr B.P. in the tropical Andes. Quatern. Res. 45: 289–299.

Herngreen, G. F. W. and H. Dueñas Jimenez. 1990. Dating of the Cretaceous Une Formation, Colombia and the relationship with the Albian–Cenomanian African–South American microfloral province. Rev. Palaeobot. Palynol. 66: 345–359.

Heusser, C. J. 1994. Pattern of glacial–interglacial vegetation in

subtropical Chile. Hist. Biol. 9: 35–45.
———. 1995a. Three late Quaternary pollen diagrams from southern Patagonia and their palaeoecological implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 118: 1–24.
———. 1995b. Palaeoecology of a *Donatia–Astelia* cushion bog, Magellanic moorland–Subantarctica evergreen forest transition, southern Tierra del Fuego, Argentina. Rev. Palaeobot. Palynol. 89: 429–440.
———. 1998. Deglacial paleoclimate of the American sector of the Southern Ocean: Late-glacial–Holocene records from the latitude of Canal Beagle (55°S), Argentine Tierra del Fuego. Palaeogeogr. Palaeoclimatol. Palaeoecol. 141: 277–301.
———. 2003. Ice Age Southern Andes: A Chronicle of Paleoecological Events. Elsevier Science Publishers, Amsterdam.
——— et al. (+ 5 authors). 1996a. Full-glacial–late-glacial palaeoclimate of the Southern Andes: Evidence from pollen, beetle and glacial records. J. Quartern. Sci. 11: 173–184.
———, G. H. Denton, A. Hauser, B. G. Andersen, and T. V. Lowell. 1996b. Water fern (*Azolla filiculoides* Lam.) in southern Chile as an index of paleoenvironment during early deglaciation. Arctic Alpine Res. 28: 148–155.
———, L. E. Heusser, and T. V. Lowell. 1999. Paleoecology of the southern Chilean Lake District—Isla Grande de Chiloé during middle–late Llanquihue glaciation and deglaciation. Geogr. Ann., Ser. A, Phys. Geogr. 81: 231–284.
Hickman, C. S. and J. H. Lipps. 1985. Geologic youth of Galápagos Islands confirmed by marine stratigraphy and paleontology. Science 227: 1578–1580.
Hilley, G. E., R. Bürgmann, A. Ferretti, F. Novali, and F. Rocca. 2004. Dynamics of slow-moving landslides from permanent scatter analysis. Science 304: 1952–1955.
Hinojosa, L. F. and C. Villagrán. 1997. Historia de los bosques del sur de Sudamérica, I: Antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. Revista Chilena Hist. Nat. 70: 225–239.
——— and ———. 2005. Did South America mixed paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic? Palaeogr. Palaeoclimatol. Palaeoecol. 217: 1–23.
Hoerling, M. P., J. W. Hurrell, and T. Xu. 2001. Tropical origins for recent North Atlantic climate change. Science 292: 90–92.
Hoffmann, G. et al. (+ 11 authors). 2003. Coherent isotope history of Andean ice cores over the last century. Geophys Res. Lett. 30: 10.1029/2002GL014870.
Hoffstetter, R. 1956. Lexique Stratigraphique International, Volumen V, Amerique Latine, Fasc. 5b, Peru. Centre National de la Recherche Scientifique, Paris.
Hollick, A. and E. W. Berry. 1924. A Late Tertiary flora from Bahia, Brazil. Johns Hopkins Univ. Stud. Geol. 5: 1–136.
Hooghiemstra, H. 1984. Vegetational and climatic history of the High Plain of Bogotá, Colombia: A continuous record of the last 3.5 million years. The Quaternary of Colombia 10: 1–368. [Reprinted from Dissertationes Botanicae, Band 79, J. Cramer, Vaduz, Germany.]
———. 1989. Quaternary and upper Pliocene glaciations and forest development in the tropical Andes: Evidence from a long high-resolution pollen record from the sedimentary basin of Bogotá, Colombia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 72: 11–26.
———. 1993. Pliocene–Quaternary paleoclimatic change and evolution of northern Andean montane forests and páramo ecosystems. Extended Abstract, Conference on Palaeoclimate and Evolution, with Emphasis on Human Origins (Warrenton, Virginia, 1993): 1–9.
———. 1994a. Paleoclimatic conditions around 3 million years BP: Pollen evidence from Colombia. U. S. Geol. Surv. Open File Report 94-23: 31–37.
———. 1994b. Pliocene–Quaternary floral migration, evolution of northern Andean ecosystems and climatic change: Implications from the closure of the Panamanian Isthmus. Profil (Institut für Geologie und Paläontologie, Universität Stuttgart) 7: 413–425.
———. 1995. Environmental and paleoclimatic evolution in late Pliocene–Quaternary Colombia. *In:* E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle (eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, CT. pp. 249–261.
———, J. L. Melice, A. Berger, and N. Shackleton. 1993. Frequency spectra and palaeoclimatic variability of the high-resolution 30–1450 ka Funza-1 pollen record (Eastern Cordillera, Colombia). Quatern. Sci. Rev. 12: 141–156.
——— and E. T. H. Ran. 1994. Late and middle Pleistocene climatic change and forest development in Colombia: Pollen record Funza-II (1–158 m core interval). Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 211–246.
——— and T. van der Hammen. 1993. Late Quaternary vegetation history and paleoecology of Laguna Pedro Palo (subandean forest belt, Eastern Cordillera, Colombia). Rev. Palaeobot. Palynol. 77: 235–262.
——— and ———. 1995. A Younger Dryas climatic event in Colombia. Proc. Kon. Ned. Akad. Wetensch., Ser. Phys. 44: 47–48.
——— and R. van't Veer. 1999. A 0.6 million year pollen record from the Colombian Andes. PAGES Newslett. 7(3): 4–5.
———, V. M. Wijninga, and A. M. Cleef. 2006. The paleobotanical record of Colombia: Implications for biogeography and biodiversity. *In:* A. Graham (ed.), Latin American Biogeography—Causes and Effects. Ann. Missouri Bot. Gard. 93: 297–325.
——— et al. (+ 7 authors). 1994. Miocene to Pleistocene geo-ecological development of Amazonian and Andean Colombia: Tectonics, basin development, migration, evolution and climatic change. Abstract, 4th European Palaeobotanical and Palynological Conference (Heerlen/Kererade, The Netherlands): 4 pp.
Hoorn, C. 1993a. Marine incursions and the influence of An-

dean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 105: 267–309.

———. 1993b. Geología del nororiente de la Amazonia Peruana: La Formacion Pebas. *In:* R. Kalliola, M. Puhakka, and W. Danjoy (eds.), Vegetación Húmeda Tropical en el Llano Subandino. Paut y Onern, Jyväskylä. pp. 69–85.

———. 1994a. Miocene palynostratigraphy and paleoenvironments of northwestern Amazonia, evidence for marine incursions and the influence of Andean tectonics. Ph.D. Dissertation, University of Amsterdam, Amsterdam.

———. 1994b. An environmental reconstruction of the palaeo–Amazon River System (middle-late Miocene, NW Amazonia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 112: 187–238.

———. 1994c. Fluvial palaeoenvironments in the intracratonic Amazonas Basin (early Miocene–early middle Miocene, Colombia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 1–54.

———. 1996. Miocene deposits in the Amazonian foreland Basin. Science 273: 122–123. [See response by Räsänen and Linna, pp. 124–125.]

Horton, B. K., B. A. Hampton, and G. L. Waanders. 2001. Paleogene synorogenic sedimentation in the Altiplano Plateau and implications for initial mountain building in the Central Andes. Geol. Soc. Amer. Bull. 113: 1387–1400.

Huang, J. L. and R. A. Price. 2003. Estimation of the age of extant *Ephedra* using chloroplast *rbcL* sequence data. Molec. Biol. Evol. 20: 435–440.

Huertas G., G. 1970. Evidencia fósil del género *Musa* en Colombia. Mutisia 33: 21–28.

———. 1977. Una Melastomatácea fósil del Terciario carbonifero de Antioquia (Eoceno). Caldasia 12: 35–39.

——— and T. van der Hammen. 1953. Un posible banana (*Musa*) fósil del Cretáceo de Colombia. Revista Acad. Colomb. Ci. Exact. 9: 115–118.

Hughen, K. A., T. I. Eglinton, L. Xu, and M. Makou. 2004. Abrupt tropical vegetation response to rapid climate changes. Science 304: 1955–1959.

———, J. T. Overpeck, L. C. Peterson, and S. Trumbore. 1996. Rapid climate changes in the tropical Atlantic region during the last deglaciation. Nature 380: 51–54.

Hunicken, M. 1955. Depositos Neocretacicos y Tertiarios del extremo SSW de Santa Cruz (Cuenca Carbonífera de Río Turbio). Anales Mus. Nac. Hist. Nat. Bernardino Rivadavia 4: 1–164.

Hurt, W. R., T. van der Hammen, and G. Correal Urrego. 1976. The El Abra rockshelters, Sabana de Bogotá, Colombia, South America. Occas. Pap. Monogr. Indiana Univ. Mus. 2: 1–56.

Ickert-Bond, S. M. and M. F. Wojciechowski. 2004. Phylogenetic relationships in *Ephedra* (Gnetales): Evidence from nuclear and chloroplast DNA sequence data. Syst. Bot. 29: 834–849.

Iglesias, A. et al. (+ 6 authors). 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. Geology 35: 947–950.

Iriate, J. 2006. Vegetation and climate change since 14,810 ^{14}C yrs B.P. in southeastern Uruguay and implications for the rise of early Formative societies. Quatern. Res. 65: 20–32.

Irion, G. et al. (+ 5 authors). 2005. Letters to the Editor [re D. Rossetti et al., 2005]. Quatern. Res. 64: 279–282.

Iriondo, M. H. 1980. El Cuaternario de Entre Ríos. Revista Asoc. Ci. Nat. Litoral 11: 125–141.

———. 1999a. Last glacial maximum and hypsithermal in the Southern Hemisphere. Quatern. Int. 62: 11–19.

———. 1999b. Climatic changes in the South American plains: Records of a continent-scale oscillation. Quatern. Int. 57/58: 93–112.

Jackson, J. B. C. and D. H. Erwin. 2006. What can we learn about ecology and evolution from the fossil record? Trends Ecol. Evol. 21: 322–328.

Jaramillo, C. A. and D. L. Dilcher. 2001. Middle Paleogene palynology of central Colombia, South America: A study of pollen and spores from tropical latitudes. Palaeontographica, Abt. B, Paläophytol. 258: 87–213.

———, M. J. Rueda, and G. Mora. 2006. Cenozoic plant diversity in the Neotropics. Science 311: 1893–1896.

Jenkyns, H. C., A. Forster, S. Schouten, and J. S. Sinninghe Damsté. 2004. High temperatures in the Late Cretaceous Arctic Ocean. Nature 432: 888–892.

Jennerjahn, T. C. et al. (+ 5 authors). 2004. Asynchronous terrestrial and marine signals of climate change during Heinrich events. Science 306: 2236–2239.

Johnson, T. C. et al. (+ 5 authors). 2002. A high-resolution paleoclimate record spanning the past 25,000 years in southern East Africa. Science 296: 113–114, 132.

Jordon, G. J. and M. K. MacPhail. 2003. A middle–late Eocene inflorescence of Caryophyllaceae from Tasmania, Australia. Amer. J. Bot. 90: 761–768.

Kaandrop, R. J. G. et al. (+ 5 authors). 2005. Seasonal Amazonian rainfall variation in the Miocene Climate Optimum. Palaeogeogr. Palaeoclimatol. Palaeoecol. 221: 1–6.

Kay, R. F. and R. H. Madden. 1997. Mammals and rainfall: Paleoecology of the middle Miocene at La Venta (Colombia, South America). J. Human Evol. 32: 161–199.

Keefer, D. K., M. E. Moseley, and S. D. deFrance. 2003. A 38,000-year record of floods and debris flows in the Ilo region of southern Peru and its relation to El Niño events and great earthquakes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 41–77.

——— et al. (+ 5 authors). 1998. Early maritime economy and El Niño events at Quebrada Tacahuay, Peru. Science 281:

1833–1835.
Kienast, M., S. Steinke, K. Stattegger, and S. E. Calvert. 2001. Synchronous tropical South China Sea SST change and Greenland warming during deglaciation. Science 291: 2132–2134.
Klammer, G. 1982. Die Palaeowuste des Pantanal von Mato Grosso und die Pleistozane Klimageschichte de Brasilianischen Randtropen. Z. Geomorphol. 26: 393–416.
Klein, A. G., G. O. Seltzer, and B. L. Isacks. 1999. Modern and last local glacial maximum snowlines in the Central Andes of Peru, Bolivia, and northern Chile. Quatern. Sci. Rev. 18: 63–84. [See also Correspondence and Reply, Quartern. Sci. Rev. (2001) 20: 1153.]
Kleinert, K. and M. R. Strecker. 2001. Climate change in response to orographic barrier uplift: Paleosol and stable isotope evidence from the late Neogene Santa María Basin, northwestern Argentina. Geol. Soc. Amer. Bull. 113: 728–742.
Knorr, G. and G. Lohmann. 2003. Southern Ocean origin for the resumption of Atlantic thermohaline circulation during deglaciation. Nature 424: 532–536.
Knowlton, F. H. 1919. Description of a supposed new fossil species of maize from Peru. J. Wash. Acad. Sci. 9: 134–136.
Kröhling, D. M. 1999. Upper Quaternary geology of the lower Carcarañá Basin, north Pampa, Argentina. Quatern. Int. 57/58: 135–148.
Kuhry, P. 1988. Palaeobotanical–palaeoecological studies of tropical high Andean peatbog sections (Cordillera Oriental, Colombia). Diss. Bot. 116: 1–241. [See also Palaeogeogr. Palaeoclimatol. Palaeoecol. 55: 19–72.]
———, H. Hooghiemstra, B. Van Geel, and T. van der Hammen. 1993. The El Abra stadial in the Eastern Cordillera of Colombia (South America). Quatern. Sci. Rev. 12: 333–343.
Kukla, G. J. et al. (+ 22 authors). 2002. Last interglacial climates. Quatern. Res. 58: 2–13.
Kumar, A. 1981. Palynology of the Pitch Lake, Trinidad, West Indies. Pollen & Spores 23: 259–272.
Kunzmann, L., B. A. R. Mohr, and M. E. C. Bernardes-de-Oliveira. 2004. Gymnosperms from the Lower Cretaceous Crato Formation (Brazil). I. Araucariaceae and *Lindleycladus* (incertae sedis). Mitt. Mus. Naturk. Berlin, Geowiss. Reihe 7: 155–174.
Kurtz, F. 1899. Contribuciones a la palaeophytologie Argentina: Sobre la existencia de una Dakota-flora en la Patagonia austro-occidental. Revista Mus. La Plata 10: 43–60.
———. 1921. Atlas de Plantas Fósiles de la República Argentina. Actas Acad. Nac. Ci. Córdoba 7: 129–153.
Lamb, S. 2004. Devil in the Mountain: A Search for the Origin of the Andes. Princeton University Press, Princeton, NJ.
Lamy, F., D. Hebbeln, and G. Wefer. 1998. Late Quaternary precessional cycles of terrigenous sediment input off the Norte Chico, Chile (27.5°S) and palaeoclimatic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 141: 233–251.
———, ———, and ———. 1999. High-resolution marine record of climatic change in mid-latitude Chile during the last 28,000 years based on terrigenous sediment parameters. Quatern. Res. 51: 83–93.
———, J. Klump, D. Hebbeln, and G. Wefer. 2000. Late Quaternary rapid climate change in northern Chile. Terra Nova 12: 8–13.
——— et al. (+ 5 authors). 2004. Antarctic timing of surface water changes off Chile and Patagonian ice sheet response. Science 304: 1959–1962.
Latorre, C., J. L. Betancourt, K. A. Rylander, J. Quade, and O. Matthei. 2003. A vegetation history from the arid prepuna of northern Chile (22–23°S) over the last 13,500 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 223–246.
——— et al. (+ 8 authors). 2005. Late Quaternary history of the Atacama Desert. *In:* M. Smith and P. Hesse (eds.), 23°S: Archaeology and Environmental History of the Southern Deserts. National Museum of Australia Press, Canberra. pp. 73–90.
Lea, D. W. 2004. The 100,000-yr cycle in tropical SST, greenhouse forcing, and climate sensitivity. J. Climatol. 17: 2170–2179.
———, P. A. Martin, D. K. Pak, and H. J. Spero. 2002. Reconstructing a 350 kyr history of sea level using planktonic Mg/Ca and oxygen isotope records from a Cocos Ridge core. Quatern. Sci. Rev. 21: 283–293.
———, D. K. Pak, L. C. Peterson, and K. A. Hughen. 2003. Synchroneity of tropical and high-latitude Atlantic temperatures over the last glacial termination. Science 301: 1361–1364.
Ledru, M.-P. 1993. Late Quaternary environmental and climatic changes in central Brazil. Quatern. Res. 39: 90–98.
———. 2002. Late Quaternary history and evolution of the cerrados as revealed by palynological records. *In:* P. O. Oliveira and R. J. Marques (eds.), The Cerrados of Brazil. Colombia University Press, New York. pp. 33–50.
———, M. L. Salgado-Labouriau, and M. L. Lorscheitter. 1998. Vegetation dynamics in southern and central Brazil during the last 10,000 years B.P. Rev. Palaeobot. Palynol. 99: 131–142.
——— et al. (+ 6 authors). 1996. The last 50,000 years in the Neotropics (southern Brazil): Evolution of vegetation and climate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 123: 239–257.
——— et al. (+ 6 authors). 2001. Late-glacial cooling in Amazonia inferred from pollen at Lagoa do Caçó, northern Brazil. Quatern. Res. 55: 47–56.
——— et al. (+ 5 authors). 2005. Paleoclimate changes during the last 100,000 years from a record in the Brazilian Atlantic rainforest region and interhemispheric comparison. Quatern. Res. 64: 444–450.
Leidelmeyer, P. 1966. The Paleocene and lower Eocene pollen flora of Guyana. Leidse Geol. Meded. 38: 49–70.
Leyden, B. W. 1985. Late Quaternary aridity and Holocene

moisture fluctuations in the Lake Valencia Basin, Venezuela. Ecology 66: 1279–1295.

———. 1989. Datos polinicos del periodo Holoceno tardio en el Lago Titikaka, Bolivia: Una posible inundación en La Pampa Koani. *In:* A. L. Kolata (ed.), Arqueología de Lukurmata, Vol. II. Instituto Nacional de Arqueología y Producciones Puma Punku, La Paz. pp. 263–274.

Lichte, M. and H. Behling. 1999. Dry and cold climatic conditions in the formation of the present landscape in southeastern Brazil, an interdisciplinary approach to a controversially discussed topic. Z. Geomorphol. 43: 341–358.

Limarino, C. et al. (+ 5 authors). 2000. Definición litoestratigráfica de la Formación Ciénaga del Río Huaco (Cretácico Superior), Precordillera Central, San Juan, Argentina. Revista Asoc. Geol. Argent. 55: 83–99.

Liu, Z. and T. D. Herbert. 2004. High-latitude influence on the eastern equatorial Pacific climate in the early Pleistocene epoch. Nature 427: 720–723.

Longobucco, M. I., C. L. Azcuy, and B. Aguirre Urreta. 1985. Plantas de la Formación Kachaike, Cretácico de la Provincia de Santa Cruz. Ameghiniana 21: 305–315.

Lorente, M. A. 1986. Palynology and Palynofacies of the Upper Tertiary in Venezuela. Dissertationes Botanicae, Band 99, J. Cramer, Berlin.

Lowell, T. V. et al. (+ 8 authors). 1995. Interhemispheric correlations of late Pleistocene glacial events. Science 269: 1541–1549.

MacFadden, B. J., Y. Wang, T. E. Cerling, and F. Anaya. 1994. South American fossil mammals and carbon isotopes: A 25-million-year sequence from the Bolivian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107: 257–268.

Malumian, N. and J. Panza. 2000. Hoja geológica yacimiento Río Turbio 5172III. Serv. Geol. Minero Bol. 247: 1–108.

Manchester, S. R. and W. J. Kress. 1993. Fossil bananas (Musaceae): *Ensete oregonense* sp. nov. from the Eocene of western North America and its phytogeographic significance. Amer. J. Bot. 80: 1264–1272.

Mancini, M. V. 1993. Recent pollen spectra from forest and steppe of south Argentina: A comparison with vegetation and climate data. Rev. Palaeobot. Palynol. 77: 129–142.

———. 1998. Vegetational changes during the Holocene in extra-Andean Patagonia, Santa Cruz Province, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 138: 207–219.

———. 2001. Análisis polínico de un sitio de altura del Holoceno tardío: Cerro Verlika 1, sudoeste de Santa Cruz, Argentina. Ameghiniana 38: 455–462.

———, M. M. Paez, and A. R. Prieto. 2002. Cambios paleoambientales durante los últimos 7.000 ^{14}C años en el ecotono bosque–estepa, 47–48°S, Santa Cruz, Argentina. Ameghiniana 39: 151–162.

——— et al. (+ 5 authors). 2005. Mid-Holocene climatic variability reconstruction from pollen records (32°–52°S, Argentina). Quatern. Int. 132: 47–59.

Marchant, R., J. C. Berrío, H. Behling, A. Boom, and H. Hooghiemstra. 2006. Colombian dry moist forest transitions in the Llanos Orientales—A comparison of model and pollen-based reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 234: 28–44.

——— et al. (+ 7 authors). 2004. Colombian vegetation at the Last Glacial Maximum: A comparison of model- and pollen-based biome reconstructions. J. Quatern. Sci. 19: 721–732.

———, A. Boom, and H. Hooghiemstra. 2002. Pollen-based biome reconstructions for the past 450,000 yr from the Funza-2 core, Colombia: Comparisons with model-based vegetation reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 177: 29–45.

Marden, C. J. 1997. Late-glacial fluctuations of south Patagonian icefield, Torres del Paine National Park, southern Chile. Quatern. Int. 38/39: 61–68.

Markgraf, V. 1991. Younger Dryas in southern South America? Boreas 20: 63–69.

———. 1993. Paleoenvironments and paleoclimates in Tierra del Fuego and southernmost Patagonia, South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 102: 53–68.

——— (ed.). 2001. Interhemispheric Climate Linkages. Academic Press, New York.

——— et al. (+ 8 authors). 2000. Paleoclimate reconstruction along the pole–equator–pole transect of the Americas (PEP 1). Quatern. Sci. Rev. 19: 125–140.

Maslin, M. A. and S. J. Burns. 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. Science 290: 2285–2287.

Matteri, C. M. 1988. Restos de *Didymodon* sp. (Pottiaceae, Musci) en sedimentos de Isla Gable, Argentina. Bol. Asoc. Latinoamer. Paleobot. Palin. 11: 23–27.

Mautino, L. R. and L. M. Anzótegui. 1998. Palinología de la Formación Chiquimil (Mioceno Superior) en Vallecito, Provincia de Catamarca, Argentina. Parte I. Esporas: Especies nuevas. Ameghiniana 35: 227–233.

——— and ———. 2000. Esporas del Mioceno y retrabajadas del Mesozoico en la Formación Chiquimil, Vallecito, Provincia de Catamarca. Ameghiniana 37: 13–22.

McCulloch, R. D. and M. J. Bentley. 1998. Late Glacial ice advances in the Strait of Magellan, southern Chile. Quatern. Sci. Rev. 17: 775–787.

McPhee, J. 1981. Basin and Range. Farrar, Straus, and Giroux, New York.

Medina-Elizalde, M. and D. W. Lea. 2005. The mid-Pleistocene transition in the tropical Pacific. Science 310: 1009–1012.

Melendi, D. L., L. Scafati, and W. Volkheimer. 2003. Palynostratigraphy of the Paleogene Huitrera Formation in N-W Patagonia, Argentina. Neues Jahrb. Geol. Paläontol. Abh. 228: 205–273.

Melief, A. B. M. 1985. Late Quaternary Paleoecology of the Parque Nacional Natural Los Nevados (Cordillera Central), and Sumapaz (Cordillera Oriental) Areas, Colombia. Ph.D. Dissertation, University of Amsterdam, Amsterdam.

Menéndez, C. A. 1960. Elementos floristicos del Terciario de

Argentina. I. *Ruprechtia latipedunculata* n. sp. del Arroyo Chenqueñiyeu, Río Negro. Acta Geol. Lilloana 3: 15–19.
———. 1961. Estípite petrificado de una nueva Cyatheaceae del Tertiario de Neuquén. Bol. Soc. Argent. Bot. 9: 331–358.
———. 1962. Leño petrificado de una leguminosa del Terciario de Tiopunco, Provincia de Tucumán. Ameghiniana 2: 121–130.
———. 1966a. Fossil Bennettitales from the Ticó flora, Santa Cruz Province, Argentina. Bull. Brit. Mus. (Nat. Hist.) Geol. 12: 1–42.
———. 1966b. La presencia de *Thyrsopteris* en el Cretácico de Cerro Guido, Chile. Ameghiniana 4: 299–302.
———. 1972a. La flora del Cretácico Superior de Cerro Guido, Chile (1–2). Ameghiniana 9: 209–212.
———. 1972b. La flora del Cretácico Superior de Cerro Guido, Chile (3–7). Ameghiniana 9: 289–297.
——— and M. A. Caccavari de Filice. 1975. Las especies de *Nothofagidites* (polen fósil de *Nothofagus*) de sedimentos Terciarios y Cretácicos de estancia La Sara, norte de Tierra del Fuego, Argentina. Ameghiniana 12: 165–183.
Miller, G. H., J. W. Magee, and A. J. T. Jull. 1997. Low-latitude glacial cooling in the Southern Hemisphere from amino-acid racemization in emu eggshells. Nature 385: 241–244.
Miotti, L. and M. Salemme. 1999. Biodiversity, taxonomic richness and specialists-generalists during late Pleistocene/early Holocene times in Pampa and Patagonia (Argentina, southern South America). Quatern. Int. 53/54: 53–68.
Mohr, B. A. R. and M. E. C. Bernardes de Oliveira. 2004. *Endressinia brasiliana*, a magnolialean angiosperm from the Lower Cretaceous Crato Formation (Brazil). Int. J. Pl. Sci. 165: 1121–1133.
——— and H. Eklund. 2003. *Araripia florifera*, a magnoliid angiosperm from the Lower Cretaceous Crato Formation (Brazil). Rev. Palaeobot. Palynol. 126: 279–292.
——— and E. M. Friis. 2000. Early angiosperms from the Lower Cretaceous Crato Formation (Brazil), a preliminary report. Int. J. Pl. Sci. 161 (6 Suppl.): S155–S167.
——— and C. Rydin. 2002. *Trifurcatia flabellata* n. gen. n. sp., a putative monocotyledon angiosperm from the Lower Cretaceous Crato Formation (Brazil). Mitt. Mus. Naturk. Berlin, Geowiss. Reihe 5: 335–344.
Molnar, P. and P. England. 1990. Late Cenozoic uplift of mountain ranges and global climate change: Chicken or egg? Nature 346: 29–34.
Monsch, K. A. 1998. Miocene fish faunas from the northwestern Amazonia Basin (Colombia, Peru, Brazil), with evidence of marine incursions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 143: 31–50.
Mora, G. and L. M. Pratt. 2001. Isotopic evidence for cooler and drier conditions in the tropical Andes during the last glacial stage. Geology 29: 519–522.
——— and ———. 2002. Carbon isotopic evidence from paleosols for mixed C_3/C_4 vegetation in the Bogotá Basin, Colombia. Quatern. Sci. Rev. 21: 985–995.
Moran, K. et al. (+ 36 authors). 2006. The Cenozoic palaeoenvironment of the Arctic Ocean. Nature 441: 601–605.
Moreno, P. I., G. L. Jacobson Jr., T. V. Lowell, and G. H. Denton. 2001. Interhemispheric climate links revealed by a late-glacial cooling episode in southern Chile. Nature 409: 804–808.
Mourguiart, Ph. et al. (+ 6 authors). 1998. Holocene palaeohydrology of Lake Titicaca estimated from an ostracod-based transfer function. Palaeogeogr. Palaeoclimatol. Palaeoecol. 143: 51–72.
Muller, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47: 1–142.
———, E. de Di Giacomo, and A. W. van Erve. 1987. A palynological zonation for the Cretaceous, Tertiary, and Quaternary of northern South America. AASP (American Association Stratigraphic Palynologists) Contrib. Ser. No. 19: 7–76.
Nash, J. M. 2002. El Niño: Unlocking the Secrets of the Master Weather-Maker. Warner Books, New York.
———. 2007. Chronicling the ice. Smithsonian 38 (July 2007): 66–74. [Long before global warming became a cause célèbre, Lonnie Thompson was extracting climate secrets from ancient glaciers. He finds the problem is even more profound than you might have thought. "What really stands out is how unusual the last 50 years have been."]
Nishida, M. 1970. On some fossil plants from Chile, South America. Annual Report, The Foreign Students' College of Chiba University 5: 13–18.
———. 1981a. Petrified woods from the Tertiary of Mocha Island (a preliminary report). Rep. Paleobot. Surv. S. Chile: 31–37.
———. 1981b. Petrified woods from the Tertiary of Quiriquina Island (a preliminary report). Rep. Paleobot. Surv. S. Chile: 38–40.
——— and H. Nishida. 1985. Petrified woods from the Upper Cretaceous of the Quiriquina Island. Rep. Bot. Surv. Bolivia and S. Chile: 27–36.
———, ———, and T. Nasa. 1988. Anatomy and affinities of the petrified plants from the Tertiary of Chile V. Bot. Mag. (Tokyo) 101: 293–309.
———, ———, and T. Ohsawa. 1989. Comparison of the petrified woods from the Cretaceous and Tertiary of Antarctica and Patagonia. Proc. Natl. Inst. Polar Res. Symp. Polar Biol. 2: 198–212.
———, T. Ohsawa, and H. Nishida. 1990. Anatomy and affinities of the petrified plants from the Tertiary of Chile (IV). Bot. Mag. (Tokyo) 103: 255–268.
———, ———, ———, and M. Rancusi H. 1992. Permineralized coniferous woods from the XI region of Chile, central Patagonia. Res. Inst. Evol. Biol. Sci. Rep. 7: 47–59.
Núñez, L., M. Grosjean, and I. Cartajena. 2002. Human occu-

pations and climate change in the Puna de Atacama, Chile. Science 298: 821–824.

Ohkouchi, N., T. I. Eglinton, L. D. Keigwin, and J. M. Hayes. 2002. Spatial and temporal offsets between proxy records in a sediment drift. Science 298: 1224–1227.

Olivero, E. B., V. Barreda, S. A. Marenssi, S. N. Santillana, and D. R. Martinioni. 1998. Estratigrafía sedimentología y palinología de la Formación Sloggett (Paleoceno continental), Tierra del Fuego. Rev. Asoc. Geol. Argent. 53: 504–516.

Ortlieb, L., A. Diaz, and N. Guzman. 1996. A warm interglacial episode during oxygen isotope stage 11 in northern Chile. Quatern. Sci. Rev. 15: 857–871.

Ortloff, C. R. and A. L. Kolata. 1993. Climate and collapse: Agro-ecological perspectives on the decline of the Tiwanaku state. J. Archaeol. Sci. 20: 195–221.

Osborn, G. et al. (+ 6 authors). 1995. Potential glacial evidence for the Younger Dryas event in the Cordillera of North and South America. Quatern. Sci. Rev. 14: 823–832.

Osborn, J. M., T. N. Taylor, and M. R. de Lima. 1993. The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. Rev. Palaeobot. Palynol. 77: 171–184.

Paduano, G. M., M. B. Bush, P. A. Baker, S. C. Fritz, and G. O. Seltzer. 2003. A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 259–279.

Paez, M. M., A. R. Prieto, and M. V. Mancini. 1999. Fossil pollen from Los Toldos locality: A record of the late-glacial transition in the extra-Andean Patagonia. Quatern. Int. 53/54: 69–75.

Pagani, M. et al. (+ 8 authors). 2006. Arctic hydrology during global warming at the Palaeocene/Eocene thermal maximum. Nature 442: 671–675.

Palamarczuk, S. and V. Barreda. 1998. Bioestratigrafía en base a quistes de dinoflagelados de la Formación Chenque (Mioceno), Provincia del Chubut, Argentina. Ameghiniana 35: 415–426.

——— and ———. 2000. Palinología del Paleogeno tardío–Neogeno temprano, pozo Aries x-1, plataforma continental Argentina, Tierra del Fuego. Ameghiniana 37: 221–234.

——— and J. C. Gamerro. 1988. *Grapnelispora evansii*, megaspora del Cretácico Superior (? Campaniano Superior–Maastrichtiano) de Argentina y Antartida. Actas 3, IV Congreso Argentino de Paleontologia y Bioestratigrafía (Mendoza, Argentina, 1986): 87–93.

Palazzesi, L. and V. Barreda. 2004. Primer registro palinológico de la Formación Puerto Madryn, Mioceno de la Provincia del Chubut, Argentina. Ameghiniana 41: 355–362.

Palma-Heldt, S. 1980a. Nuevos antecedentes en el estudio palinológico de los mantos carboníferos del Terciario de Arauco–Concepción, Chile. Bol. Inst. Geoci. Univ. São Paulo 11: 33: 161–168.

———. 1980b. Contribución al conocimiento palinológico de los mantos carboniferous del Terciario de Arauco–Concepción, Chile. Actas II Congreso Argent. Paleontol. y I Congreso Latinoamer. Paleontol. (Buenos Aires, 1978): 175–192.

———. 1983. Estudio palinológico del Terciario sedimentario de Lonquimay, Provincia de Malleco, Chile. Revista Geol. Chile 18: 55–75.

Papu, O. H. 1988. Estudio palinológico de la Formación Paso del Sapo (Cretácico Superior) en la localidad de "Los Fortines," Valle Medio del Río Chubut. Parte I: Esporas triletes laevigati y apiculati. Parte II: Esporas triletes murornati, tricrassati y esporas monoletes. Actas 3, IV Congreso Argentino de Paleontología y Bioestratigrafía (Mendoza, Argentina, 1986): 63–73, 75–85.

———. 1990. Contribución a la palinología estratigráfica de la Formación Malargüe, Cretácico Superior, sur de la Provincia de Mendoza, Argentina. Parte 1: Especies terrestres y de aguas continentales. Ameghiniana 27: 289–303.

Pardo-Trujillo, A., C. A. Jaramillo, and F. E. Oboh-Ikuenobe. 2003. Paleogene palynostratigraphy of the eastern Middle Magdalena Valley, Colombia. Palynology 27: 155–178.

Pares Regali, M. d. S., N. Uesugui, and A. d. S. Santos. 1974. Palinológia dos sedimentos Meso-Cenozóicos do Brasil (I). Bol. Técn. Petrobrás 17: 177–191. (II). 17: 263–301.

Passalia, M. G., S. Archangelsky, E. J. Romero, and G. Cladera. 2003. A new early angiosperm leaf from the Anfiteatro de Ticó Formation (Aptian), Santa Cruz Province, Argentina. Revista Mus. Argent. Ci. Nat. 5: 245–252.

———, E. J. Romero, and J. L. Panza. 2001. Improntas foliares del Cretácico de la Provincia de Santa Cruz, Argentina. Ameghiniana 38: 73–84.

Pastorino, M. J. and L. A. Gallo. 2002. Quaternary evolutionary history of *Austrocedrus chilensis*, a cypress native to the Andean–Patagonian forest. J. Biogeogr. 29: 1167–1178.

Pennington, R. T., D. E. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. J. Biogeogr. 27: 261–273.

Perry, L. et al. (+ 6 authors). 2006. Early maize agriculture and interzonal interaction in southern Peru. Nature 440: 76–79.

Person, C. P. and T. Delevoryas. 1982. The Middle Jurassic flora of Oaxaca, Mexico. Palaeontographica, Abt. B, Paläophytol. 180: 82–119.

Pessanda, L. C. R. et al. (+ 5 authors). 2004. Vegetation dynamics during the late Pleistocene in the Barreirinhas region, Maranhão State, northeastern Brazil, based on carbon isotopes in soil organic matter. Quatern. Res. 62: 183–193.

Petriella, B. 1969. *Menucoa cazaui* nov. gen. et sp., tronco petrificado de Cycadales, Provincia de Río Negro, Argentina. Ameghiniana 6: 291–302.

———. 1972. Estudio de maderas petrificadas del Terciario inferior del area central de Chubut (Cerro Bororo). Revista Mus. La Plata 6: 159–254.

——— and S. Archangelsky. 1975. Vegetación y ambiente en el Paleoceno de Chubut. Actas I Congreso Argentino Paleontología y Bioestragrafía (Tucumán, Argentina, 1975):

257–270.
Placzek, C., J. Quade, and P. J. Patchett. 2006. Geochronology and stratigraphy of late Pleistocene lake cycles on the southern Bolivian Altiplano: Implications for causes of tropical climate change. Geol. Soc. Amer. Bull. 118: 515–532.
Pons, D. 1965. Contribution a l'étude de la flore fossile de Colombie. Bol. Geol. Univ. Industr. Santander 20: 61–87.
———. 1969. A propos d'une Goupiacee du Tertiaire de Colombie: *Goupioxylon stutzeri* Schönfeld. Palaeontographica, Abt. B, Paläophytol. 128: 65–80.
———. 1971. Sur un bois fossile du Mésozoïque de la Colombie: *Protophyllocladoxylon rosablancaense* n. sp. Rev. Palaeobot. Palynol. 11: 101–123.
———. 1975. A propos d'une fougere Tertiaire de Colombie: *Cyathea colombiensis* D. Pons. Argum. Palaeobot. 4: 39–44.
———. 1976. Sur une empreinte fossile de Moraceae (Formation Mesa, Colombie). Actes 101e Congrès Nat. Soc. Savantes (Lille, France, 1976) 1: 121–134.
———. 1977. *Muntingiophyllum calaburoides* nov. gen., nov. sp., Elaeocarpaceae fossile de la Formation Mesa (Colombie). Compt. Rend. 102e Congrès Nat. Soc. Savantes (Limoges, France, 1977) 1: 171–185.
———. 1978. *Calophyllites mesaensis* nov. gen., nov. sp., Guttiferae fossile de Falan (Formation Mesa, Colombie). Actes Congrès Nat. Soc. Savantes (Nancy, France, 1978) 2: 201–209.
———. 1979. *Coussapoites portae* sp. nov., Moraceae fossile de la Formation Mesa (Tertiaire Supérieur de Colombie). Compt. Rend. 104e Congrès Nat. Soc. Savantes (Bordeaux, France, 1979) 1: 331–339.
———. 1980. Les bois fossils du Tertiaire Supérieur de la région de Toluviejo–Corozal (Dépt. de Sucre, Colombie). Actes 105e Congrès Nat. Soc. Savantes (Caen, France, 1980) 1: 163–182.
———. 1983. *Lecythidospermum bolivarensis* (Berry) nov. comb., graine fossile de Lecythidaceae (Angiosperme) du Tertiare de la Colombie. Ann. Paléontol. 69: 1–12.
———. 1984. La flore du Bassin Houiller d'Antioquia (Tertiaire de Colombie). Actes 109e Congrès Nat. Soc. Savantes (Dijon, France, 1984) II: 37–56.
———. 1985. Types biologiques foliaires et paléoenvironnements (Tertiaire de la moyenne Magdalena, Colombia). Bull. Sect. Sci. 8: 235–257.
———. 1988. Le Mésozoïque de Colombie, Macroflores et Microflores. Centre National de la Recherche Scientifique, Paris.
Poole, I., D. Cantrill, and T. Utescher. 2005. A multi-proxy approach to determine Antarctic terrestrial palaeoclimate during the Late Cretaceous and Early Tertiary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 222: 95–121.
Poore, R. Z. and H. J. Dowsett. 2001. Pleistocene reduction of polar ice caps: Evidence from Cariaco Basin marine sediments. Geology 29: 71–74.
Por, F. D. 1995. The Pantanal of Mato Grosso (Brazil): World's Largest Wetlands. Kluwer Academic Publishers, Dordrecht, The Netherlands.
Prámparo, M. B., O. H. Papú, and J. P. Milana. 1996. Estudio palinológico del miembro inferior de la Formación Pachaco, Terciario de la Provincia de San Juan. Descripciones sistemáticas. Ameghiniana 33: 397–407.
——— and W. Volkheimer. 2002. Nuevos hallazgos de palinomorfos en la Formación La Amarga, Miembro Bañados de Cachigüe, Cuenca Neuquina sudoriental, Argentina. Ameghiniana 39: 395–404.
Prance, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichatetalaceae and Lecythidaceae. Acta Amazon. 3: 5–28.
——— (ed.). 1982. Biological Diversification in the Tropics. Columbia University Press, New York.
Premoli, A. C., T. Kitzberger, and T. T. Veblen. 2000. Isozyme variation and recent biogeographic history of the long-lived conifer *Fitzroya cupressoides*. J. Biogeogr. 27: 251–260.
Prieto, A. R. 2000. Vegetational history of the Late Glacial–Holocene transition in the grasslands of eastern Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 157: 167–188.
———, A. M. Blasi, C. G. De Francesco, and C. Fernández. 2004. Environmental history since 11,000 ^{14}C yrs B.P. of the northeastern Pampas, Argentina, from alluvial sequences of the Luján River. Quatern. Res. 62: 146–161.
Prous, A. and E. Fogaça. 1999. Archaeology of the Pleistocene–Holocene boundary in Brazil. Quatern. Int. 53/54: 21–41.
Quattrocchio, M. 1978a. Contribución al conocimiento de la palinológia estratigráfica de la Formación Lumbrera (Terciario Inferior, Grupo Salta). Ameghiniana 15: 285–300.
———. 1978b. Datos paleoecológicos y paleoclimatológicos de la Formación Lumbrera (Grupo Salta). Ameghiniana 15: 173–181.
——— and A. M. Borromei. 1998. Paleovegetational and paleoclimatic changes during the late Quaternary in southwestern Buenos Aires Province and southern Tierra del Fuego (Argentina). Palynology 22: 67–82.
———, R. Marquillas, and W. Volkheimer. 1988. Palinología, paleoambientes y edad de la Formación Tunal Cuenca del Grupo Salta (Cretácico–Eoceno), República Argentina. Actas 3, IV Congreso Argentino de Paleontologia y Bioestratigrafia (Mendoza, Argentina, 1986): 95–107.
——— and L. C. Ruiz. 1999. Paleoambiente de la Formación Pedro Luro (Maastrichtiano?–Paleoceno) en base a palinomorfos, Cuenca del Colorado, Argentina. Ameghiniana 36: 37–47.
——— and W. Volkheimer. 1988. Microflora de los estratos limitrofes entre Cretácico y Terciario en las localidades de Tilian y Corralito, Cuenca del Grupo Salta. Descripciones sistemáticas. Actas 3, IV Congreso Argentine de Paleontología y Bioestratigrafía (Mendoza, Argentina, 1986): 109–120.

——— and ———. 1990. Paleogene paleoenvironmental trends as reflected by palynological assemblage types, Salta Basin, NW Argentina. Neues Jahrb. Geol. Paläontol. Abh. 181: 377–396.

——— and ———. 2000. Danian microfloral provinces in Argentina. Revista Esp. Paleontol. 15: 3–11.

———, ———, and C. del Papa. 1997. Palynology and paleoenvironment of the "Faja Gris" Mealla Formation (Salta Group) at Garabatal Creek (NW Argentina). Palynology 21: 231–247.

Rabassa, J. et al. (+ 10 authors). 2000. Quaternary of Tierra del Fuego, southernmost South America: An updated review. Quatern. Int. 68–71: 217–240.

Ramirez, E. et al. (+ 12 authors). 2003. A new Andean deep ice core from Nevado Illimani (6350 m), Bolivia. Earth Planet. Sci. Lett. 212: 337–350.

Räsänen, M. 1991. History of the fluvial and alluvial landscapes of the western Amazon forelands. Dissertation, Ser. A, 75, Annales Universatis Turkuensis, Turku, Finland.

———, A. M. Linna, J. C. R. Santos, and F. R. Negri. 1995. Late Miocene tidal deposits in the Amazonian foreland Basin. Science 269: 386–390.

———, R. Neller, J. Salo, and H. Jungner. 1992. Recent and ancient fluvial depositional systems in the Amazonian foreland Basin, Peru. Geol. Mag. 129: 293–306.

Rech, J. A., J. S. Pigati, J. Quade, and J. L. Betancourt. 2003. Re-evaluation of mid-Holocene deposits at Quebrada Puripica, northern Chile. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 207–222.

———, J. Quade, and J. L. Betancourt. 2002. Late Quaternary paleohydrology of the central Atacama Desert (lat 22°–24°S), Chile. Geol. Soc. Amer. Bull. 114: 334–348.

Reid, E. M. 1933. Note on some fossil fruits of Tertiary age from Colombia, South America. Rev. Géogr. Phys. Géol. Dynam. (Université de Paris) 6: 209–214. [Citation in Appendix 2 under Tertiary (undifferentiated).]

Rigsby, C. A., P. A. Baker, and M. S. Aldendefer. 2003. Fluvial history of the Río Llave Valley, Peru, and its relationship to climate and human history. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 165–185.

———, J. Platt Bradbury, P. A. Baker, S. M. Rollins, and M. R. Warren. 2005. Late Quaternary palaeolakes, rivers, and wetlands on the Bolivian Altiplano and their palaeoclimatic implications. J. Quatern. Sci. 20: 671–691.

Rittenour, T. M., J. Brigham-Grette, and M. E. Mann. 2000. El Niño-like climate teleconnections in New England during the late Pleistocene. Science 288: 1039–1042.

Rodbell, D. T. et al. (+ 5 authors). 1999. An ~15,000-year record of El Niño-driven alluviation in southwestern Ecuador. Science 283: 516–520.

Rodriguez, J. A. 2005. Human occupation of the eastern La Plata Basin and the adjacent littoral region during the mid-Holocene. Quatern. Int. 132: 23–36.

Romero, E. J. 1968. *Palmoxylon patagonicum* n. sp., del Terciario inferior de la Provincia de Chubut, Argentina. Ameghiniana 5: 417–432.

———. 1970. *Ulminium atlanticum* n. sp. tronco petrificado de Lauraceae del Eoceno de Bahia Solano, Chubut, Argentina. Ameghiniana 7: 205–224.

———. 1977. Polen de gimnospermas y fagáceas de la Formación Río Turbio (Eoceno), Santa Cruz, Argentina. Fundacíon para la Educación, La Ciencia y La Cultura, Buenos Aires.

———. 1978. Paleoecología y paleofitogeografía de las tafofloras del Cenofitico de Argentina y areas vecinas. Ameghiniana 15: 209–227.

———. 1986. Paleogene phytogeography and climatology of South America. Ann. Missouri Bot. Gard. 73: 449–461.

———. 1993. South American paleofloras. *In:* P. Goldblatt (ed.), Biological Relationships between Africa and South America. Yale University Press, New Haven, CT. pp. 62–85.

——— and S. Archangelsky. 1986. Early Cretaceous angiosperm leaves from southern South America. Science 234: 1580–1582.

——— and M. H. Arguijo. 1981a. Austrosudamerica. *In:* Comite Sudamerico del Jurásico y Cretácico (eds.), Cuencas Sedimentarias del Jurásico y Cretácico de América del Sur 2: 393–406.

——— and ———. 1981b. Adición a la tafoflora del yacimiento "Bariloche" (Eoceno), Provincia de Río Negro, República Argentina. Anais II Congresso Latino-Americano Paleontologia (Porto Alegre, 1981): 489–495.

——— and M. T. Castro. 1986. Material fúngico y granos de polen de angiospermas de la Formacíon Río Turbio (Eoceno), Provincia de Santa Cruz, República Argentina. Ameghiniana 23: 101–118.

———, M. C. Dibbern, and M. A. Gandolfo. 1988. Revisión de *Lomatia bivascularis* (Berry) Frenguelli (Proteaceae) del yacimiento de La Laguna del Hunco (Paleoceno), Provincia del Chubut. Actas 3, IV Congreso Argentino de Paleontologie y Bioestratigrafia (Mendoza, Argentina, 1986): 125–130.

——— and L. J. Hickey. 1976. A fossil leaf of Akaniaceae from Paleocene beds in Argentina. Bull. Torrey Bot. Club 103: 126–131.

——— and M. del C. Zamaloa. 1985. Polen de angiospermas de la Formación Río Turbio (Eoceno), Provincia de Santa Cruz, República Argentina. Ameghiniana 22: 43–51.

Rossetti, D. de F., P. M. de Toledo, and A. M. Góes. 2005. New geological framework for western Amazonia (Brazil) and implications for biogeography and evolution. Quatern. Res. 63: 78–89.

Ruiz, L. C. and M. E. Quattrocchio. 1993. *Srivastavapollenites exoticus* nov. gen. et sp. de la Formación Pedro Luro (Paleoceno), Cuenca del Colorado, Argentina. Ameghiniana 30: 311–315.

——— and ———. 1997a. Estudio palinológico de la Formación Pedro Luro (?Maastrichtiano–Paleoceno) en la Cuenca del Colorado, República Argentina. Parte 1: Es-

poras triletes, laevigati, murornati, tricassati, cingulati y zonati. Revista Esp. Micropaleontol. 29: 13–29.

——— and ———. 1997b. Estudio palinológico de la Formación Pedro Luro (?Maastrichtiano–Paleoceno) en la Cuenca del Colorado, República Argentina. Parte 2: Truma saccites, plicates, poroses e Incertae Sedis. Revista Esp. Micropaleontol. 29: 115–137.

Rull, V. 1991. Contribución a la paleoecología de Pantepui y la Gran Sabana (Guayana Venezolana): Clima, biogeografía y ecología. Sci. Guianae 2: 1–133.

———. 1998. Palaeoecology of pleniglacial sediments from the Venezuelan Andes. Palynological record of El Caballo stadial, sedimentation rates and glacier retreat. Rev. Palaeobot. Palynol. 99: 95–114.

———. 2005. Vegetation and environmental constancy in the Neotropical Guayana Highlands during the last 6000 years? Rev. Palaeobot. Palynol. 135: 205–222.

——— et al. (+ 5 authors). 2005. 15,000-yr pollen record of vegetation change in the high altitude tropical Andes at Laguna Verde Alta, Venezuela. Quatern. Res. 64: 308–317.

———, M. L. Salgado-Labouriau, C. Schubert, and S. Valastro Jr. 1987. Late Holocene temperature depression in the Venezuelan Andes: Palynological evidence. Palaeogeogr. Palaeoclimatol. Palaeoecol. 60: 109–121.

Rydin, C., B. Mohr, and E. M. Friis. 2003. *Cratonia cotyledon* gen. et sp. nov.: A unique Cretaceous seedling related to *Welwitschia*. Proc. Roy. Soc. London, Ser. B (Suppl.): 1–4.

———, K. R. Pedersen, and E. M. Friis. 2004. On the evolutionary history of *Ephedra*: Cretaceous fossils and extant molecules. Proc. Natl. Acad. Sci. U.S.A. 101: 16,571–16,576.

Sachs, J. P. and R. F. Anderson. 2005. Increased subantarctic ocean productivity during Heinrich events. Nature 434: 1118–1121.

Salgado-Labouriau, M. L. (ed.). 1973. Contribuição à Palinología dos Cerrados. Academia Brasileira de Ciências, Rio de Janeiro.

———. 1980. A pollen diagram of the Pleistocene–Holocene boundary of Lake Valencia, Venezuela. Rev. Palaeobot. Palynol. 30: 297–312.

———. 1984. Late-Quaternary palynological studies in the Venezuelan Andes. Erdwiss. Forsch. 18: 279–293.

———. 1986. Late Quaternary paleoecology of Venezuelan high mountains. *In:* F. Vuilleumier and M. Monasterio (eds.), High Altitude Tropical Biogeography. Oxford University Press, Oxford, U.K. pp. 202–216.

———. 1987/1988. Sequence of colonization by plants in the Venezuelan Andes after the last Pleistocene glaciation. J. Palynol. 23–24: 189–204.

———. 1991a. Vegetation and climatic changes in the Merida Andes during the last 13,000 years. Bol. Inst. Geoci. Univ. São Paulo, Publ. Espec. 8: 159–170.

———. 1991b. Palynology of the Venezuelan Andes. Grana 30: 342–349.

———, M. Barberi, K. R. Ferraz-Vicentini, and M. G. Parizzi. 1998. A dry climatic event during the late Quaternary of tropical Brazil. Rev. Palaeobot. Palynol. 99: 115–129.

———, R. S. Bradley, R. Yuretich, and B. Weingarten. 1992. Paleoecological analysis of the sediments of Lake Mucubaji, Venezuelan Andes. J. Biogeogr. 19: 317–327.

——— et al. (+ 6 authors). 1997. Late Quaternary vegetational and climatic changes in cerrado and palm swamp from central Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 128: 215–226.

———, V. Rull, C. Schubert, and S. Valastro Jr. 1988. The establishment of vegetation after late Pleistocene deglaciation in the Páramo de Miranda, Venezuelan Andes. Rev. Palaeobot. Palynol. 55: 5–17.

Sanaiotti, T. M., L. A. Martinelli, R. L. Victoria, S. E. Trumbore, and P. B. Camargo. 2002. Past vegetation changes in Amazon savannas determined using carbon isotopes of soil organic matter. Biotropica 34: 2–16.

Sandweiss, D. H. 2003. Terminal Pleistocene through mid-Holocene archaeological sites as paleoclimate archives for the Peruvian coast. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 23–40.

——— et al. (+ 5 authors). 2001. Variation in Holocene El Niño frequencies: Climate records and cultural consequences in ancient Peru. Geology 29: 603–606.

Schäbitz, F. 1994. Holocene climatic variations in northern Patagonia, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 287–294.

Schofield, E. K. and P. A. Colinvaux. 1969. Fossil *Azolla* from the Galapagos Islands. Bull. Torrey Bot. Club 96: 623–628.

Schönfeld, G. 1947. Hölzer aus dem Tertiär von Kolumbien. Abh. Senckenberg. Naturf. Ges. 475: 1–53.

Schreve-Brinkman, E. J. 1978. A palynological study of the upper Quaternary sequence in the El Abra corridor and rock shelters (Colombia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 25: 1–109.

Schubert, C. 1979. La zona del páramo: Morfología glacial y periglacial de Los Andes de Venezuela. *In:* M. L. Salgado-Labouriau (ed.), El Medio Ambiente Páramo. Ediciones Centro de Estudios Avanzados, Caracas. pp. 11–27.

———, P. Fritz, and R. Aravena. 1992. Investigaciones paleoambientales: Resultados preliminaries. *In:* O. Huber (ed.), Chimantá, Escudo de Guayana, Venezuela, Un Ensayo Ecológico Tepuyano. Oscar Todtmann Editores, Caracas. pp. 97–130.

——— and O. Huber. 1989. The Gran Sabana: Panorama of a Region. Lagoven Booklets, Caracas.

Schubert, S. D., M. J. Suarez, P. J. Pegion, R. D. Koster, and J. T. Bacmeister. 2004. On the cause of the 1930s dust bowl. Science 303: 1855–1859.

Schuler, M. and J. Doubinger. 1970. Observations palynologiques dans le Bassin d'Amaga (Colombie). Pollen & Spores 12: 429–450.

Scotese, C. R. 2004. Cenozoic and Mesozoic paleogeography: Changing terrestrial biogeographic pathways. *In:* M. V. Lo-

molino and L. R. Heaney (eds.), Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland, MA. pp. 9–26.

Seltzer, G. O. 2001. Workshop Reports: Paleoclimates of the Central Andes. PAGES Newsl. 9: 16.

———, P. Baker, S. Cross, P. Dunbar, and S. C. Fritz. 1998. High-resolution seismic reflection profiles from Lake Titicaca, Peru–Bolivia: Evidence for Holocene aridity in the tropical Andes. Geology 26: 167–170.

——— and D. T. Rodbell. 2005. Delta progradation and neoglaciation, Laguna Parón, Cordillera Blanca, Peru. J. Quatern. Sci. 20: 715–722.

——— et al. (+ 6 authors). 2002. Early warming of tropical South America at the last glacial–interglacial transition. Science 296: 1685–1686.

Servant, M. and S. Servant-Vildary. 2003. Holocene precipitation and atmospheric changes inferred from river paleowetlands in the Bolivian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 187–206.

Shackleton, N., M. Chapman, M. F. Sánchez–Goñi, and D. Pailler. 2002. The classic marine isotope substage 5e. Quatern. Res. 58: 14–16.

Sinanoglu, E. 1983. Early Cretaceous palynomorphs from the Zuata Area, eastern Venezuela. Contrib. IV Reuniâo Paleobotânicos Palinólogos (Universidade de São Paulo, Brasil, 1983): 129–140.

Singewald, J. T., Jr. and E. W. Berry. 1922. The geology of the Corocoro Copper District of Bolivia. Johns Hopkins Univ. Stud. Geol. 1: 1–117.

Smith, A. G., D. G. Smith, and B. M. Funnell. 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge, U.K.

Smith, J. A., R. C. Finkel, D. L. Farber, D. T. Rodbell, and G. O. Seltzer. 2005a. Moraine preservation and boulder erosion in the tropical Andes: Interpreting old surface exposure ages in glaciated valleys. J. Quatern. Sci. 20: 735–758.

———, G. O. Seltzer, D. T. Rodbell, and A. G. Klein. 2005b. Regional synthesis of last glacial maximum snowlines in the tropical Andes, South America. Quatern. Int. 138/139: 145–167.

———, ———, D. L. Faber, D. T. Rodbell, and R. C. Finkel. 2005c. Early local Last Glacial Maximum in the tropical Andes. Science 308: 678–681.

Solé de Porta, N. 1960. Observaciones palinológicas sobre el Plioceno de Cartagena (Colombia). Bol. Geol. Univ. Industr. Santander 4: 45–53.

———. 1961. Contribución a la palinología del Tertiario del norte de Colombia. Servicio Geológico Nacional (Bogotá) Informe No. 1351, Bol. Geol. 8: 75–94.

———. 1963. Asociación esporo–polinica hallada en una serie perteneciente a la Formación La Cira del Valle del Magdalena (Colombia). Servicio Geológico Nacional (Bogotá) Informe No. 1351, Bol. Geologico 11: 5–16.

———. 1971. Algunos generos nuevos de polen procedentes de la Formación Guaduas (Maastrichtiense)–Paleoceno de Colombia. Studia Geológica (Salamanca) 2: 133–143.

———. 1972. Palinología de la Formación Cimarrona (Maastrichtiense) en el Valle Medio del Magdalena, Colombia. Stud. Geol. (Salamanca) 4: 103–142.

Soltis, D. E., P. S. Soltis, P. K. Endress, and M. V. Chase. 2005. Phylogeny and Evolution of Angiosperms. Sinauer Associates, Sunderland, MA.

Soltis, P. S. and D. E. Soltis. 2004. The origin and diversification of angiosperms. Amer. J. Bot. 91: 1614–1626.

Sombroeck, W. G. 1966. Amazon Soils: A Reconnaissance of the Soils of the Amazon Basin Region. Wageningen Center for Agricultural Publications, Wageningen, The Netherlands.

Steeves, M. W. and E. S. Barghoorn. 1959. The pollen of *Ephedra*. J. Arnold Arbor. 40: 221–255.

Steig, E. J. 2006. The south-north connection. Nature 444: 152–153.

——— et al. (+ 8 authors). 1998. Synchronous climate changes in Antarctica and the North Atlantic. Science 282: 92–95.

Stockey, R. A. 1977. Reproductive biology of the Cerro Cuadrado (Jurassic) fossil conifers: *Paraucaria patagonica*. Amer. J. Bot. 64: 733–744.

———. 1978a. On the structure and evolutionary relationships of the Cerro Cuadrado fossil conifer seedlings. Bot. J. Linn. Soc. 76: 161–176.

———. 1978b. Reproductive biology of Cerro Cuadrado fossil conifers: Ontogeny and reproductive strategies in *Araucaria mirabilis* (Spegazzini) Windhausen. Palaeontographica, Abt. B, Paläophytol. 166: 1–15.

———. 1982. The Araucariaceae: An evolutionary perspective. Rev. Palaeobot. Palynol. 37: 133–154.

Stoner, J. S., C. Laj, J. E. T. Channell, and C. Kissel. 2002. South Atlantic and North Atlantic geomagnetic paleointensity stacks (0–80 ka): Implications for inter-hemispheric correlation. Quatern. Sci. Rev. 21: 1141–1151.

Stough, J. B. 1968. Palynomorphs from South America. University of Kansas Paleontological Contributions Paper 32: 1–12.

Stutz, S., A. R. Prieto, and F. I. Isla. 2002. Historia de la vegetación del Holoceno de la Laguna Hinojales, sudeste de la provincial de Buenos Aires, Argentina. Ameghiniana 39: 85–94.

Stuut, J.-B. W. and F. Lamy. 2004. Climate variability at the southern boundaries of the Namib (southwestern Africa) and Atacama (northern Chile) coastal deserts during the last 120,000 yr. Quatern. Res. 62: 301–309.

Suguio, K. 1980. Síntese dos conhecimentos sobre a sedimentação da Bacia de São Paulo. *In:* Mesa Redonda sobre Aspectos Geológicos de Geotécnicos da Bacia Sedimentar de São Paulo. Publ. Esp. ABGE-SBG, São Paulo. pp. 25–32.

Sylvestre, F. et al. (+ 5 authors). 1999. Lake-level chronology on the southern Bolivian Altiplano (18°–23°S) during late-glacial time and the early Holocene. Quatern. Res. 51: 54–66.

Takahashi, K. 1978. Upper Cretaceous palynofossils from Quiriquina Island, Chile. J. Palynol. 14: 30–49.

Tanai, T. and M. Nishida. 1981. Paleobotanical bibliographies in Chile (excluding the Quaternary). Rep. Paleobot. Surv. S. Chile 49–50.

Tapia, P. M., S. C. Fritz, P. A. Baker, G. O. Seltzer, and R. B. Dunbar. 2003. A late Quaternary diatom record of tropical climatic history from Lake Titicaca (Peru and Bolivia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 139–164.

Tauber, A. A. 1997a. Bioestratigrafía de la Formación Santa Cruz (Mioceno Inferior) en el extreme sudeste de la Patagonia. Ameghiniana 34: 413–426.

———. 1997b. Paleoecología de la Formación Santa Cruz (Mioceno Inferior) en el extremo sudeste de la Patagonia. Ameghiniana 34: 517–529.

Taylor, T. N. and S. Archangelsky. 1985. The Cretaceous pteridosperms *Ruflorinia* and *Ktalenia* and implications on cupule and carpel evolution. Amer. J. Bot. 72: 1842–1853.

———, M. S. Zavada, and S. Archangelsky. 1987. The ultrastructure of *Cyclusphaera psilata* from the Cretaceous of Argentina. Grana 26: 74–80.

Thompson, L. G., M. E. Davis, E. Moseley-Thompson, and K.-b. Liu. 1988. Pre-Incan agricultural activity recorded in dust layers in two tropical ice cores. Nature 336: 763–765.

———, ———, ———, P.-n. Lin, K. A. Henderson, and T. A. Mashiotta. 2005. Tropical ice core records: Evidence for asynchronous glaciation on Milankovitch timescales. J. Quatern. Sci. 20: 723–733.

———, L. Hastenrath, and B. Arnao. 1979. Climate ice core records from the tropical Quelccaya ice cap. Science 203: 1240–1243.

——— and E. Moseley-Thompson. 1987. Evidence of abrupt climatic change during the last 1500 years recorded in ice cores from the tropical Quelccaya ice cap. *In:* W. Berger and L. Labeyrie (eds.), Abrupt Climatic Change: Evidence and Implications. D. Reidel Publishing Co., Dordrecht, The Netherlands. pp. 99–110.

——— and ———. 1989. One-half millennia of tropical climate variability as recorded in the stratigraphy of the Quelccaya ice cap, Peru. *In:* D. H. Peterson (ed.), Aspects of Climate Variability in the Pacific and the Western Americas. AGU Geophysical Union Monogr. (Washington, D.C.) 55: 15–31.

———, ———, J. F. Bolzan, and B. R. Koci. 1985. A 1500-year record of tropical precipitation in ice cores from the Quelccaya ice cap, Peru. Science 229: 971–973.

———, ———, and B. Morales Arnao. 1984. Major El Nino/Southern Oscillation events recorded in stratigraphy of the tropical Quelccaya ice cap. Science 226: 50–52.

——— et al. (+ 5 authors). 1982. Geophysical investigations of the tropical Quelccaya ice-cap. J. Glaciol. 28: 57–68.

——— et al. (+ 7 authors). 1995. Late glacial stage and Holocene tropical ice core records from Huascarán, Peru. Science 269: 46–50.

——— et al. (+ 11 authors). 1998. A 25,000-year tropical climate history from Bolivian ice cores. Science 282: 1858–1864.

Thouret, J.-C., T. van der Hammen, B. Salomons, and E. Juvigné. 1996. Paleoenvironmental changes and glacial stades of the last 50,000 years in the Cordillera Central, Colombia. Quatern. Res. 46: 1–18.

Tonni, E. P. et al. (+ 8 authors). 1999. The Ensenada and Buenos Aires formations (Pleistocene) in a quarry near La Plata, Argentina. J. S. Amer. Earth Sci. 12: 273–291.

Torres, V., J. Vandenberghe, and H. Hooghiemstra. 2005. An environmental reconstruction of the sediment infill of the Bogotá Basin (Colombia) during the last 3 million years from abiotic and biotic proxies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 226: 127–148.

Trauth, M. H., B. Bookhagen, N. Marwan, and M. R. Strecker. 2003. Multiple landslide clusters record Quaternary climate changes in the northwestern Argentine Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 109–212.

——— and M. R. Strecker. 1999. Formation of landslide-dammed lakes during a wet period between 40,000 and 25,000 yr B.P. in northwestern Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 153: 277–287.

Traverso, N. E. 1966. *Brachyphyllum tigrense*, nueva conífera de la Formación Baqueró, Cretácico de Santa Cruz. Ameghiniana 4: 189–194.

Troncoso A., A. 1991. Paleomegaflora de la Formación Navidad, miembro Navidad (Mioceno), en el area de Matanzas, Chile central occidental. Bol. Mus. Nac. Hist. Nat. Chile 42: 131–168.

———. 1992. La tafoflora Terciaria de Quinamavida (VII Region, Chile). Bol. Mus. Nac. Hist. Nat. Chile 43: 155–178.

——— and E. J. Romero. 1993. Consideraciones acerca de las coníferas del Mioceno de Chile central occidental. Bol. Mus. Nac. Hist. Nat. Chile 44: 47–71.

Tryon, R. M. and A. F. Tryon. 1982. Ferns and Allied Plants, with Special Reference to Tropical America. Springer Verlag, Berlin.

Uemura, K. 1990. Tertiary plants from the Guadal area in Aisén region, Chile. Rep. Paleobotan. Surv. Patagonia, Chile (1989): 8–11.

Vajda, V., J. I. Raine, and C. J. Hollis. 2001. Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. Science 294: 1700–1702.

——— and S. McLoughlin. 2004. Fungal proliferation at the Cretaceous–Tertiary boundary. Science 303: 1489.

Vajda-Santivanez, V. 1999. Miospores from Upper Cretaceous–Paleocene strata in northwestern Bolivia. Palynology 23: 181–196.

Valero-Garcés, B. L., M. Grosjean, K. Kelts, H. Schreier, and B. Messerli. 1999. Holocene lacustrine deposition in the Atacama Altiplano: Facies models, climate and tectonic forcing. Palaeogeogr. Palaeoclimatol. Palaeoecol. 151: 101–125.

——— et al. (+ 6 authors). 2005. Palaeohydrology of Laguna

de Tagua Tagua (34°30'S) and moisture fluctuations in central Chile for the last 46,000 yr. J. Quatern. Sci. 20: 625–641.

van der Hammen, T. (ed.). 1995. Pliocene y Cuaternario del Altiplano de Bogotá y Alrededores. Analisis Geograficos No. 24. Instituto Geografico Agustin Codazzi, Santafé de Bogotá, D.C., Colombia.

——— and D. Burger. 1966. Pollen flora and age of the Takutu Formation, Guyana. Leidse Geol. Meded. 38: 173–180.

——— and G. Correal Urrego. 1978. Prehistoric man on the Sabana de Bogotá: Data for an ecological prehistory. Palaeogeogr. Palaeoclimatol. Palaeoecol. 25: 179–190.

——— and G. Garcia de Mutis. 1966. The Paleocene pollen flora of Colombia. Leidse Geol. Meded. 35: 105–116.

——— and H. Hooghiemstra. 1995. The El Abra stadial, a Younger Dryas equivalent in Colombia. Quatern. Sci. Rev. 14: 841–851.

——— and T. A. Wijmstra. 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. Leidse Geol. Meded. 30: 183–241.

van Geel, B. and T. van der Hammen. 1973. Upper Quaternary vegetational and climatic sequence of the Fuquene area (Eastern Cordillera, Colombia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 14: 9–92. [Also in *The Quaternary of Colombia*, Vol. 1.]

van't Veer, R. and H. Hooghiemstra. 2000. Montane forest evolution during the last 650,000 yr in Colombia: A multivariate approach based on pollen record Funza-1. J. Quatern. Sci. 15: 329–346.

———, G. A. Islebe, and H. Hooghiemstra. 2000. Climatic change during the Younger Dryas chron in northern South America: A test of the evidence. Quatern. Sci. Rev. 19: 1821–1835.

———, E. T. H. Ran, H. J. P. M. Mommersteeg, and H. Hooghiemstra. 1995. Multivariate analysis of the middle and late Pleistocene Funza pollen records of Colombia. Meded. Rijks Geol. Dienst. 52: 195–212.

Vanzolini, P. E. and E. E. Williams. 1970. South American anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. São Paulo 19: 1–298.

Veit, H. 1996a. Holocene landscape and climate evolution of the Central Andes. Zentrabl. Geol. Paläontol. 7/8: 887–895.

———. 1996b. Southern westerlies during the Holocene deduced from geomorphological and pedological studies in the Norte Chico, northern Chile (27–33°S). Palaeogeogr. Palaeoclimatol. Palaeoecol. 123: 107–119.

Vélez, M. I., H. Hooghiemstra, S. Metalfe, M. Wille, and J. C. Berrío. 2006. Late Glacial and Holocene environmental and climate changes from a limnological transect through Colombia, northern South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 234: 81–96.

Verzi, D. H. and C. A. Quintana. 2005. The caviomorph rodents from the San Andrés Formation, east-central Argentina, and global late Pliocene climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 219: 303–320.

Vidal, L. et al. (+ 5 authors). 1999. Link between the North and South Atlantic during the Heinrich events of the last glacial period. Clim. Dynam. 15: 909–919.

Villagrán M., C. 1980. Vegetationgeschichtliche und pflanzensoziologische Untersuchungen im Vicente Pérez Rosales National Park (Chile). Dissertationes Botanicae, Band 54, J. Cramer, Vanduz, Germany.

Villa-Martínez, R., C. Villagrán, and B. Jenny. 2003. The last 7500 cal. yr B.P. of westerly rainfall in central Chile inferred from a high-resolution pollen record from Laguna Aculeo (34°S). Quatern. Res. 60: 284–293.

Villar de Seoane, L. 1997. Comparative study between *Ginkgoites tigrensis* Archangelsky and *Ginkgo biloba* Linn. leaves. The Palaeobotanist 46: 1–12.

———. 2001. Cuticular study of Bennettitales from the Springhill Formation, Lower Cretaceous of Patagonia, Argentina. Cretaceous Res. 22: 461–479.

Wallace, A. R. 1849. On the monkeys of the Amazon. Proc. Zool. Soc. London 20: 107–110.

Wang, Y. et al. (+ 9 authors). 2005. The Holocene Asian monsoon: Links to solar changes and North Atlantic climate. Science 308: 854–857.

Wanntorp, L., J. Praglowski, and E. Grafström. 2004a. New insights into the pollen morphology of the genus *Gunnera* (Gunneraceae). Grana 43: 15–21 [Cited in Appendix 2.2].

———, M. E. Dettmann, and D. M. Jarzen. 2004b. Tracking the Mesozoic distribution of *Gunnera*: Comparison with the fossil pollen species *Tricolpites reticulatus* Cookson. Rev. Palaeobot. Palynol. 132: 163–174 [Cited in Appendix 2.2].

Wara, M. W., A. C. Ravelo, and M. L. Delaney. 2005. Permanent El Niño-like conditions during the Pliocene warm period. Science 309: 758–761. [See also Kerr (2005), Additional References.]

Webster, P. and N. Streten. 1978. Late Quaternary ice age climates of tropical Australasia: Interpretations and reconstructions. Quatern. Res. 10: 279–309.

Weigend, M. 2002. Observations on the biogeography of the Amotape–Huancabamba zone in northern Peru. Bot. Rev. 68: 38–54.

Weng, C., M. B. Bush, J. S. Athens. 2002. Holocene climate change and hydrach succession in lowland Amazonian Ecuador. Rev. Palaeobot. Palynol. 120: 73–90.

———, ———, and M. R. Silman. 2004. An analysis of modern pollen rain on an elevational gradient in southern Peru. J. Trop. Ecol. 20: 113–124.

Wijmstra, T. A. 1971. The Palynology of the Guiana Coastal Basin. Drukkerij de Kempenaer, Oegstgeest, The Netherlands.

Wijninga, V. M. 1995. A first approximation of montane forest development during the Late Tertiary in Colombia. *In:* S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn (eds.), Biodiversity and Conservation of Neotropical Montane

Forests. New York Botanical Garden, Bronx. pp. 23–34.
———. 1996a. Paleobotany and Palynology of Neogene Sediments from the High Plain of Bogotá (Colombia), Evolution of the Andean Flora from a Paleoecological Perspective. Ph.D. Dissertation, University of Amsterdam, The Netherlands. [Printed in the series *The Quaternary of Colombia*, Vol. 21, and various parts published in the citations below.]
———. 1996b. Neogene ecology of the Salto de Tequendama site (2475 m altitude, Cordillera Oriental, Colombia): The paleobotanical record of montane and lowland forests. Rev. Palaeobot. Palynol. 92: 97–156.
———. 1996c. A Pliocene *Podocarpus* forest mire from the area of the high plain of Bogotá (Cordillera Oriental, Colombia). Rev. Palaeobot. Palynol. 92: 157–205.
———. 1996d. Palynology and paleobotany of the early Pliocene section Río Frío 17 (Cordillera Oriental, Colombia): Biostratigraphical and chronostratigraphical implications. Rev. Palaeobot. Palynol. 92: 329–350.
——— and P. Kuhry. 1990. A Pliocene flora from the Subachoque Valley (Cordillera Oriental, Colombia). Rev. Palaeobot. Palynol. 62: 249–290.
——— and ———. 1993. Late Pliocene paleoecology of the Guasca Valley (Cordillera Oriental, Colombia). Rev. Palaeobot. Palynol. 78: 69–127.
Wilf, P. et al. (+ 5 authors). 2003. High plant diversity in Eocene South America: Evidence from Patagonia. Science 300: 122–125.
——— et al. (+ 5 authors). 2005. Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. Amer. Naturalist 165: 634–650.
Wille, M., H. Hooghiemstra, H. Behling, K. van der Borg, and A. J. Negret. 2001. Environmental change in the Colombian subandean forest belt from 8 pollen records: The last 50 Kyr. Veg. Hist. Archaeobot. 10: 61–77.
———, J. A. Negret, and H. Hooghiemstra. 2000. Paleoenvironmental history of the Popayán area since 27,000 years B.P. at Timbio, southern Colombia. Rev. Palaeobot. Palynol. 109: 45–63.
———, H. Hooghiemstra, B. van Geel, H. Behling, A. de Jong, and K. van der Borg. 2003. Submillennium-scale migrations of the rainforest–savanna boundary in Colombia: ^{14}C wiggle-matching and pollen analysis of core Las Margaritas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 193: 201–223.
Williams, R. S., Jr. and J. G. Ferrigno (eds.). 1998. Satellite image atlas of glaciers of the world. Glaciers of South America. U.S. Geol. Surv. Prof. Paper 1386-I: 1–206.
Willis, K. J., L. Gillson, and T. M. Brncic. 2004. How "virgin" is virgin rainforest? Science 304: 402–403. [See also Response, Letters, Science 305, 13 August 2004.]
Wilson, L. R. 1959. Geological history of the Gnetales. Oklahoma Geol. Notes 19: 35–50.
Wolfe, B. B., R. Aravena, M. B. Abbott, G. O. Seltzer, and J. J. Gibson. 2001. Reconstruction of paleohydrology and paleohumidity from oxygen isotope records in the Bolivian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 176: 177–192.
Wolff, T., S. Mulitza, H. Arz, J. Pätzold, and G. Wefer. 1998. Oxygen isotopes versus CLIMAP (18 ka) temperatures: A comparison from the tropical Atlantic. Geology 26: 675–678.
Wu, S. Q. 1999. A preliminary study of the Jehol flora from western Liooning. *In:* P. J. Chen and F. Jin (eds.), Jehol Biota. Science and Technology Press, Anhui, People's Republic of China. pp. 7–57.
Yacobaccio, H. D. and M. Morales. 2005. Mid-Holocene environment and human occupation of the Puna (Susques, Argentina). Quatern. Int. 132: 5–14.
Yang, Y., B.-Y. Geng, D. L. Dilcher, Z.-D. Chen, and T. A. Lott. 2005. Morphology and affinities of an Early Cretaceous *Ephedra* from China. Amer. J. Bot. 92: 231–241.
Ybert, J.-P. 1992. Ancient lake environments as deduced from pollen analysis. *In:* C. DeJoux and A. Iltis (eds.), Lake Titicaca: A Synthesis of Limnological Knowledge. Kluwer Academic Publishers, Boston. pp. 49–62.
Yoshida, A. 1990. Preliminary notes of the palynological remnants from Mina Ligorio Marquez, Chile Chico, Chile. A Report of the Paleobotanical Survey to Patagonia, Chile (1989): 12–15.
Zamaloa, M. del C. 1996. Asociación zigósporas de Zygnemataceae (Chlorophyta) en el Terciario medio de Tierra del Fuego, Argentina. Ameghiniana 33: 179–184.
———. 2000. Palinoflora y ambiente en el Terciario del nordeste de Tierra del Fuego, Argentina. Revista Mus. Argent. Ci. Nat., n.s., 2: 43–51.
——— et al. (+ 5 authors). 2006. Casuarinaceae from the Eocene of Patagonia, Argentina. Int. J. Pl. Sci. 167: 1279–1289.
——— and E. J. Romero. 1990. Some spores and pollen from the Cullen Formation (upper Eocene to middle Oligocene), Tierra del Fuego, Argentina. Palynology 14: 123–133.
Zárate, M., G. Neme, and A. Gil. 2005. Mid-Holocene paleoenvironments and human occupation in southern South America. Quatern. Int. 132: 1–3.
Zavada, M. S. and S. E. de Villiers. 2000. Pollen of the Asteraceae from the Paleocene–Eocene of South Africa. Grana 39: 39–45.
Zetter, R., M. Hesse, and A. Frosch-Radivo. 2001. Early Eocene zona-aperturate pollen grains of the *Proxapertites* type with affinity to Araceae. Rev. Palaeobot. Palynol. 117: 267–279.
Zinck, J. A. and J. M. Sayago. 1999. Loess–paleosol sequence of La Mesada in Tucumán province, northwest Argentina characterization and paleoenvironmental interpretation. J. S. Amer. Earth Sci. 12: 293–310.
——— and ———. 2001. Climatic periodicity during the late Pleistocene from a loess–paleosol sequence in northwest Argentina. Quatern. Int. 78: 11–16.

ADDITIONAL REFERENCES/GENERAL READINGS

South America–Africa

Anhuf, D. et al. (+ 12 authors). 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239: 510–527.

Burnham, R. J., B. Ellis, and K. R. Johnson. 2005. Modern tropical forest taphonomy: Does high biodiversity affect paleoclimatic interpretations? Palaios 20: 439–451.

Fanton, J. C. M., F. Ricardi-Branco, D. Dilcher, and M. Bernardes-de-Oliveira. 2006. *Iara iguassu*, a new taxon of aquatic angiosperm from the Crato palaeoflora (Lower Cretaceous, Santana Formation, Araripe Basin, northeastern Brazil). Geociências 25: 211–216.

George, W. and R. Lavocat (eds.). 1993. The Africa–South America Connection. Clarendon Press, Oxford, U.K.

Gheerbrant, E. and J.-C. Rage. 2006. Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? Palaeogeogr. Palaeoclimatol. Palaeoecol. 241: 224–246.

Goldblatt, P. (ed.). 1993. Biological Relationships between Africa and South America. Yale University Press, New Haven, CT.

Kowalski, E. A. 2002. Mean annual temperature estimation based on leaf morphology: A test from tropical South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 188: 141–165.

Lel, M. E. 2004. The African Rain Forest During the Last Glacial Maximum, An Archipelago of Forests in a Sea of Grass. Ph.D. Dissertation, Wageningen University, Wageningen, The Netherlands.

Marchant, R. and H. Hooghiemstra. 2004. Rapid environmental change in African and South American tropics around 4000 years before present: A review. Earth Sci. Rev. 66: 217–260.

Meggers, B. J., E. S. Ayensu, and D. Duckworth. 1973. Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Institution Press, Washington, D.C.

Servant, M. et al. (+ 6 authors). 1993. Tropical forest changes during the late Quaternary in African and South American lowlands. Global Planet. Change 7: 25–40.

Sifeddine, A. et al. (+ 6 authors). 2004. Bulk composition of sedimentary organic matter used in palaeoenvironmental reconstructions: Examples from the tropical belt of South America and Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 214: 41–53. [See also Stuut and Lamy, 2004, References section.]

Teleconnections

Ariztegui, D., F. S. Anselmetti, K. Kelts, G. O. Seltzer, and K. D'Agostino. 2001. Identifying paleoenvironmental change across South and North America using high-resolution seismic stratigraphy in lakes. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 227–240.

Baker, P. A. 2002. Trans-Atlantic climate connections. Science 296: 67–68.

Billups, K. 2004. Low-down on a rhythmic high. Nature 427: 686–687. [...the effects of a high-latitude cycle evidently reached into the tropics.]

Boninsegna, J. A. and M. K. Hughes. 2001. Volcanic signals in temperature reconstructions based on tree-ring records for North and South America. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 141–154.

Bradbury, J. P., M. Grosjean, S. Stine, and F. Sylvestre. 2001. Full and Late Glacial lake records along the PEP 1 transect: Their role in developing interhemispheric paleoclimate interactions. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 265–291.

Broecker, W. S. and S. Hemming. 2001. Climate swings come into focus. Science 294: 2308–2309.

Chiang, J. C. H. and A. Koutavas. 2004. Tropical flip-flop connections. Nature 432: 684–685.

Dokken, T. M. and K. H. Nisancioglu. 2004. Fresh angle on the polar seesaw. Nature 430: 842–843. [Summary of Knutti et al. (2004) article below.]

Evans, M. N., R. G. Fairbanks, and J. L. Rubenstone. 1998. A proxy index of ENSO teleconnections. Nature 394: 732–733.

Fritz, S. C., S. E. Metcalfe, and W. Dean. 2001. Holocene climate patterns in the Americas inferred from paleolimnological records. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 241–263.

Grimm, E. C., S. Lozano-García, H. Behling, and V. Markgraf. 2001. Holocene vegetation and climate variability in the Americas. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 325–370.

Kaufmann, R. K. and D. I. Stern. 1997. Evidence for human influence on climate from hemispheric temperature relations. Nature 388: 39–44.

Kerr, R. A. 2003. Who pushed whom out of the last ice age? Science 299: 1645.

Knutti, R., J. Flückiger, T. F. Stocker, and A. Timmermann. 2004. Strong hemispheric coupling of glacial climate through freshwater discharge and ocean circulation. Nature 430: 851–856.

Lea, D. W. 2001. Ice ages, the California Current, and Devils Hole. Science 293: 59–60.

Ledru, M.-P. and P. Mourguiart. 2001. Late glacial vegetation records in the Americas and climatic implications. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 371–390.

Markgraf, V. and G. O. Seltzer. 2001. Pole–Equator–Pole paleoclimates of the Americas integration: Toward the big picture. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 433–442.

Peterson, L. C., G. H. Haug, K. A. Hughen, and U. Röhl. 2000.

Rapid changes in the hydrologic cycle of the tropical Atlantic during the last glacial. Science 290: 1947–1951.
Poulsen, C. J. 2004. A balmy Arctic. Nature 432: 814–815.
Ribbe, J. 2004. The southern supplier. Nature 427: 23–24. [Physical processes in the Southern Ocean largely control nutrient distribution in the global marine environment, a finding that further highlights the influence of this oceanic region on Earth's climate.]
Schmidt, M. W., H. J. Spero, and D. W. Lea. 2004. Links between salinity variation in the Caribbean and North Atlantic thermohaline circulation. Nature 428: 160–163.
Shackleton, N. 2001. Climate change across the hemispheres. Science 291: 58–59.
Sirocko, F. 2003. What drove past teleconnections? Science 301: 1336–1337.
Stocker, T. F. 2002. North-South connections. Science 297: 1814–1815.
———. 2003. South dials north. Nature 424: 496–499. [Climate is greatly influenced by ocean circulation in the North Atlantic. But warming episodes, as glacial conditions turned into interglacials, may have been triggered by events far to the south.]
Wang, X. et al. (+ 7 authors). 2004. Wet periods in northeastern Brazil over the past 210 Kyr linked to distant climate anomalies. Nature 432: 740–743.
White, J. W. C. and E. J. Steig. 1998. Timing is everything in a game of two hemispheres. Nature 394: 717–718. [... rapid warming events happening first in the Southern Hemisphere.]
Whitlock, C., P. J. Bartlein, V. Markgraf, and A. C. Ashworth. 2001. The midlatitudes of North and South America during the Last Glacial Maximum and early Holocene: Similar paleoclimate sequences despite differing large-scale controls. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 391–416.

Other References/Readings

Absy, M. L. et al. (+ 10 authors). 1991. Mise en évidence de quatre d'ouverture de la foret dense dans le sud—est de l'Amazonie au cours des 60,000 dernières années. Première comparaison avec d'autres regions tropicales. Compt. Rend. Acad. Sci. Paris 312: 673–678.
Albert, J. S., N. R. Lovejoy, and W. G. R. Crampton. 2006. Miocene tectonism and the separation of cis- and trans-Andean river basins: Evidence from Neotropical fishes. J. S. Amer. Earth Sci. 21: 14–27.
Andrus, C. F. T., D. E. Crowe, D. H. Sandweiss, E. J. Reitz, and C. S. Romanek. 2002. Otolith $\delta^{18}O$ record of mid-Holocene sea surface temperatures in Peru. Science 295: 1508–1511. [See also Comment and Response, Science 299, p. 5604.]
Archangelsky, S. 1970. Evolución de los estudios paleobotánicos en Argentina desde sus origens hasta nuestros dias. Bol. Acad. Nac. Ci. 48: 551–557.
——— and A. Archangelsky. 2005. *Aequitriradites* Delcourt & Sprumont y *Couperisporites* Pocock, esporas de hepáticas, en el Cretácico temprano de Patagonia, Argentina. Revista Mus. Argent. Ci. Nat., n.s., 7: 119–138.
——— and ———. 2006. Putative Early Cretaceous pteridaceous spores from the offshore Austral Basin in Patagonia, Argentina. Cretaceous Res. 27: 473–486.
——— and L. Lezama. 2000. Catálogo de los tipos y material ilustrado de la colección paleobotánica del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Bol. Acad. Nac. Cien. 64: 117–146.
Ashworth, A. C. and J. W. Hoganson. 1993. The magnitude and rapidity of climate change marking the end of the Pleistocene in the mid-latitudes of South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 101: 263–270.
———, V. Markgraf, and C. Villagrán. 1991. Late Quaternary climatic history of the Chilean Channels based on fossil pollen and beetle analyses, with an analysis of the modern vegetation and pollen rain. J. Quatern. Sci. 6: 279–291.
Auler, A. S. et al. (+ 8 authors). 2006. U-series dating and taphonomy of Quaternary vertebrates from Brazilian caves. Palaeogeogr. Palaeoclimatol. Palaeoecol. 240: 508–522.
Axelrod, D. I., M. T. Kalin Arroyo, and P. H. Raven. 1991. Historical development of temperate vegetation in the Americas. Revista Chilena Hist. Nat. 64: 413–446.
Baied, C. A. and J. C. Wheeler. 1993. Evolution of high Andean puna ecosystems: Environment, climate, and culture change over the last 12,000 years in the Central Andes. Mountain Res. Dev. 13: 145–156.
Baker, P. A., S. C. Fritz, J. Garland, and E. Ekdahl. 2005. Holocene hydrologic variation at Lake Titicaca, Bolivia/Peru, and its relationship to North Atlantic climate variation. J. Quatern. Sci. 20: 655–662.
Barreda, V. and S. Archangelsky. 2006. The southernmost record of tropical pollen grains in the mid-Cretaceous of Patagonia, Argentina. Cretaceous Res. 27: 778–787.
———, C. Limarino, L. Fauqué, A. Trifaldi, and L. Net. 2003. Primer registro palinológico del miembro inferior de la Formación Cerro Morado (Mioceno), Precordillera de La Rioja. Ameghiniana 40: 81–87.
Barrett, P. J., F. Florindo, and A. K. Cooper (eds.). 2006. Antarctic climate evolution: Geologic records from the margin and modelling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 231: 1–259.
Barrientos, G. and S. I. Perez. 2005. Was there a population replacement during the last mid-Holocene in the southeastern pampas of Argentina? Archaeological evidence and paleoecological basis. Quatern. Int. 132: 95–105.
Barth, O. M., C. F. Pinto da Luz, and V. L. Gomes-Klein. 2005. Pollen morphology of Brazilian species of *Cayaponia* Silva Manso (Cucurbitaceae, Cucurbiteae). Grana 44: 129–136.
Beck, J. W., J. Récy, F. Taylor, R. L. Edwards, and G. Cabioch. 1997. Abrupt changes in early Holocene tropical sea surface temperature derived from coral records. Nature 385: 705–707. [6.5° C cooler at 10,350 calendar years ago.]
Behling, H. 1995. Investigations into the late Pleistocene and

Holocene history of vegetation and climate in Santa Catarina (S Brazil). Veg. Hist. Archaeobot. 4: 127–152.

———. 1995. A high resolution Holocene pollen record from Lago do Pires, SE Brazil: Vegetation, climate and fire history. J. Paleolimnol. 14: 253–268.

———, R. R. B. Negrelle, and P. A. Colinvaux. 1997. Modern pollen rain data from the tropical Atlantic rain forest, Reserva Volta Velha, south Brazil. Rev. Palaeobot. Palynol. 97: 287–299.

———, A. J. Negret, and H. Hooghiemstra. 1998. Late Quaternary vegetational and climatic change in the Popayán region, southern Colombian Andes. J. Quatern. Sci. 13: 43–53.

———, V. D. Pillar, and S. G. Bauermann. 2005. Late Quaternary grassland (campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in western Rio Grande do Sul (southern Brazil). Rev. Palaeobot. Palynol. 133: 235–248.

Berrío, J. C., M. V. Arbeláez, J. F. Duivenvoorden, A. M. Cleef, and H. Hooghiemstra. 2003. Pollen representation and successional vegetation change on the sandstone plateau of Araracuara, Colombian Amazonia. Rev. Palaeobot. Palynol. 126: 163–181.

———, H. Behling, and H. Hooghiemstra. 2000. Tropical rain-forest history from the Colombian Pacific area: A 4200-year pollen record from Laguna Jotaordó. The Holocene 10: 749–756.

Bertels, A. 1979. Paleobiogeografía de los foraminiferos del Cretácico Superior de América del Sur. Ameghiniana 16: 273–356.

Betancourt, J. L. 2000. The Amazon reveals its secrets—partly. Science 290: 2274–2275.

Bowen, M. 2005. Thin Ice: Unlocking the Secrets of Climate in the World's Highest Mountains. Henry Holt, New York. [Studies by Lonnie Thompson; see review by Georg Hoffman, Science 438: 157.]

Bracco, R., L. del Puerto, H. Inda, and C. Castiñeira. 2005. Mid-Holocene cultural and environmental dynamics in eastern Uruguay. Quatern. Int. 132: 37–45.

Bradley, R. S., M. V. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. Science 312: 1755–1756. [Climate models predict that greenhouse warming will cause temperatures to rise faster at higher than at lower altitudes. In the tropical Andes, glaciers may soon disappear, with potentially grave consequences for water supplies.]

Brenner, G. J. 1968. Middle Cretaceous spores and pollen from northeastern Peru. Pollen & Spores 10: 341–383.

Broecker, W. S. 1995. Cooling the tropics. Nature 376: 212–213.

———. 1996. Glacial climate in the tropics. Science 272: 1902–1904.

Bush, M. B. and M. R. Silman. 2004. Observations on late Pleistocene cooling and precipitation in the lowland Neotropics. J. Quatern. Sci. 19: 677–684.

——— et al. (+ 11 authors). 2001. Paleotemperature estimates for the lowland Americas between 30°S and 30°N at the last glacial maximum. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 293–306.

Charles, C. 1997. Cool tropical punch of the ice ages. Nature 385: 681–683.

Chen, L. and S. R. Manchester. 2007. Seed morphology of modern and fossil *Ampelocissus* (Vitaceae) and implications for phytogeography. Amer. J. Bot. 94: 1534–1553. [*A. bravoi* Berry (Eocene of Peru) is similar to one group of Old World extant species.]

Chin, G. 2003. Not as dry as dust. Science 301: 567. [Reference to Nevado Illimani ice core, Ramírez et al., 2003.]

Cohen, M., P. Filho, R. Lara, H. Behling, and R. Angulo. 2005. A model of Holocene mangrove development and relative sea-level changes on the Brangança Peninsula (northern Brazil). Wetlands Ecol. Managem. 13: 433–443.

Coltorti, M. et al. (+ 5 authors). 1998. The last occurrence of Pleistocene megafauna in the Ecuadorian Andes. J. S. Amer. Earth Sci. 11: 581–586.

Cortegoso, V. 2005. Mid-Holocene hunters in the Andes Mountains: Environment, resources and technological strategies. Quatern. Int. 132: 71–80.

De Freitas, H. A. et al. (+ 5 authors). 2001. Late Quaternary vegetation dynamics in the southern Amazon Basin inferred from carbon isotopes in soil organic matter. Quatern. Res. 55: 39–46.

Denny, M. W., B. L. Lockwood, and G. N. Somero. 2009. Can the giant snake predict palaeoclimate? Nature 460: E3–E4.

Dernbach, U., W. Jung, and A. Selmeir. 1992. *Araucaria*. D'Oro Verlag, Lorsch, Germany. [Describes and illustrates Jurassic *Araucaria* from the Cerro Cuadrado petrified forest in Patagonia, Argentina, including the polished *Araucaria* cones popular with collectors.]

De Silva, S. L. and G. A. Zielinski. 1998. Global influence of the AD 1600 eruption of Huaynaputina, Peru. Nature 393: 455–458.

Falcon-Lang, H. J. 2000. The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for palaeoclimatic studies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 160: 317–328. ["Growth rings in modern conifer woods were quantitatively analysed to investigate the relationship between leaf longevity and the markedness of the growth ring boundary (including *Araucaria araucana*). These data suggest that leaf longevity exerts an important control on growth ring markedness, in addition to the influence exerted by the growing environment (climatic and edaphic conditions). The significance of these results for the paleoclimatic analysis of growth rings in fossil woods is discussed…."]

Farber, D. L., G. S. Hancock, R. C. Finkel, and D. T. Rodbell. 2005. The age and extent of tropical alpine glaciation in

the Cordillera Blanca, Peru. J. Quatern. Sci. 20: 759–776.
Fesq-Martin, M., A. Friedmann, M. Peters, J. Behrmann, and R. Kilian. 2004. Late-glacial and Holocene vegetation history of the Magellanic rain forest in southwestern Patagonia, Chile. Veg. Hist. Archaeobot. 13: 249–255.
Ficcarelli, G. et al. (+ 8 authors). 1997. Hypothesis on the cause of extinction of the South American mastodonts. J. S. Amer. Earth Sci. 10: 29–38.
Flannery, T. 2001. North American devastation or global cataclysm? Science 294: 1668–1669.
Gallego, L. and R. A. Distel. 2004. Phytolith assemblages in grasses native to central Argentina. Ann. Bot. 94: 865–874.
García, A. 2005. Human occupation of the Central Andes of Argentina (32°–34°S) during the mid-Holocene. Quatern. Int. 132: 61–70.
Gayó, E., L. F. Hinojosa, and C. Villagrán. 2005. On the persistence of tropical paleofloras in central Chile during the early Eocene. Rev. Palaeobot. Palynol. 137: 41–50.
Genise, J. F., J. C. Sciutto, J. H. Laza, M. G. González, and E. S. Bellosi. 2002. Fossil bee nests, coleopteran pupal chambers and tuffaceous paleosols from the Late Cretaceous Laguna Palacios Formation, central Patagonia (Argentina). Palaeogeogr. Palaeoclimatol. Palaeoecol. 177: 215–235.
Gil, A., M. Zárate, and G. Neme. 2005. Mid-Holocene paleoenvironments and the archeological record of southern Mendoza, Argentina. Quatern. Int. 132: 81–94.
Gnecco, C. 1999. An archaeological perspective of the Pleistocene/Holocene boundary in northern South America. Quatern. Int. 53/54: 3–9.
Graf, K. 1992. Pollendiagramme aus den Anden, eine Synthese zur Klimageschichte und Vegetationsentwicklung seit der letzten Eiszeit. Phys. Geogr. 34: 1–138.
Haberle, S. G. 1997. Upper Quaternary vegetation and climate history of the Amazon Basin: Correlating marine and terrestrial pollen records. Proc. Ocean Drilling Progr. 155: 381–396.
——— and K. D. Bennett. 2001. Modern pollen rain and lake mud–water interface geochemistry along environmental gradients in southern Chile. Rev. Palaeobot. Palynol. 117: 93–107.
Hajibabaei, M., J. Xia, and G. Drouin. 2006. Seed plant phylogeny: Gnetophytes are derived conifers and a sister group to Pinaceae. Molec. Phylogen. Evol. 40: 208–217.
Head, J. J. et al. (+ 7 authors). 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. Nature 457: 715–717.
———. 2009. Reply [to Denny et al., 2009; Makarieva et al., 2009; Sniderman, 2009]. Nature 460: E4.
Helmens, K. F., P. Kuhry, N. W. Rutter, K. van der Borg, and A. F. M. de Jong. 1996. Warming at 18,000 yr B.P. in the tropical Andes. Quatern. Res. 45: 289–299.
———, N. W. Rutter, and P. Kuhry. 1997. Glacier fluctuations in the Eastern Andes of Colombia (South America) during the last 45,000 radiocarbon years. Quatern. Int. 38/39: 39–48.
Hendy, E. J. et al. (+ 5 authors). 2002. Abrupt decrease in tropical Pacific sea surface salinity at end of Little Ice Age. Science 295: 1511–1514.
Heusser, C. J. 1994a. Paleoindians and fire during the late Quaternary in southern South America. Revista Chilena Hist. Nat. 67: 435–443.
———. 1994b. Quaternary paleoecology of Fuego–Patagonia. Revista IG São Paulo 15: 7–26.
———. 1995. Palaeoecology of a *Donatia–Astelia* cushion bog, Magellanic moorland–Subantarctic evergreen forest transition, southern Tierra del Fuego, Argentina. Rev. Palaeobot. Palynol. 89: 429–440.
———, G. H. Denton, A. Hauser, B. G. Andersen, and T. V. Lowell. 1995. Quaternary pollen records from the Archipiélago de Chiloé in the context of glaciation and climate. Revista Geol. Chile 22: 25–46.
——— et al. (+ 5 authors). 1996. Full-glacial–late-glacial palaeoclimate of the Southern Andes: Evidence from pollen, beetle and glacial records. J. Quatern. Sci. 11: 173–184.
——— and J. Rabassa. 1991. Late Holocene forest-steppe interaction at Cabo San Pablo, Isla Grande de Tierra del Fuego, Argentina. Quatern. S. Amer. Ant. Penins. 9: 173–182.
———, ———, A. Brandani, and R. Stuckenrath. 1988. Late-Holocene vegetation of the Andean *Araucaria* region, province of Neuquén, Argentina. Mountain Res. Developm. 8: 53–63.
Hocquenghem, A.-M. and L. Ortlieb. 1992. Eventos El Niño y lluvias anormales en la costa del Perú: Siglos XVI–XIX. Bull. Inst. Franç. Études Andines 21: 197–278.
Hoffmann, G. 2003. Taking the pulse of the tropical water cycle. Science 301: 776–777.
Holmes, P. L. (ed.). 1991. The Plant Fossil Record Database, Version 1.0. International Organization of Paleobotany, London.
Hooghiemstra, H. 2002. The dynamic rainforest ecosystem on geological, Quaternary and human time scales. *In:* P. Verweij (ed.), Understanding and Capturing the Multiple Values of Tropical Forests. Tropenbos International, Wageningen, The Netherlands. pp. 7–19.
———, J. L. Melice, A. Berger, and N. J. Shackleton. 1993. Frequency spectra and paleoclimatic variability of the high-resolution 30–1450 ka Funza I pollen record (Eastern Cordillera, Colombia). Quatern. Sci. Rev. 12: 141–156.
——— and G. Sarmiento. 1991. Long continental pollen record from a tropical intermontane basin: Late Pliocene and Pleistocene history from a 540-meter core. Episodes 14: 107–115.
——— and T. van der Hammen. 2004. Quaternary ice-age dynamics in the Colombian Andes: Developing an understanding of our legacy. Philos. Trans., Ser. B 349: 173–181.
Hoorn, C. and H. Vonhof (guest eds.). 2006. New contributions on Neogene geography and depositional environ-

ments in Amazonia. J. S. Amer. Earth Sci. 21: 1–172.
Hostetler, S. W. and A. C. Mix. 1999. Reassessment of ice-age cooling of the tropical ocean and atmosphere. Nature 399: 673–676.
——— and P. U. Clark. 2000. Tropical climate at the Last Glacial Maximum inferred from glacier mass-balance modeling. Science 290: 1747–1750.
Iriarte, J. et al. (+ 5 authors). 2004. Evidence for cultivar adoption and emerging complexity during the mid-Holocene in the La Plata Basin. Nature 432: 614–617. [Southeastern Uruguay.]
Iriondo, M. H. and N. O. Garcia. 1993. Climatic variations in the Argentine plains during the last 18,000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 101: 209–220.
Janzen, D. H. and P. S. Martin. 1981. Neotropical anachronisms: The fruits that the gomphotheres ate. Science 215: 19–27.
Jenny, B. et al. (+ 5 authors). 2002. Early to mid-Holocene aridity in central Chile and the southern westerlies: The Laguna Aculeo record (34°S). Quatern. Res. 58: 160–170.
Kaiser, J. 2001. Galápagos takes aim at alien invaders. Science 293: 590–592.
Kerr, R. A. 1995. Chilly ice-age tropics could signal climate sensitivity. Science 267: 961.
———. 1997. Moderating a tropical debate. Science 276: 1793.
———. 1999. El Niño grew strong as cultures were born. Science 283: 467–468.
———. 2005. El Niño or La Niña? The past hints at the future. Science 309: 687.
———. 2006. Looking way back for the world's climate future. Science 312: 1456–1457.
Kim, J-H., R. R. Schneider, D. Hebbeln, P. J. Müller, and G. Wefer. 2002. Last deglacial sea-surface temperature evolution in the southeast Pacific compared to climate changes on the South American continent. Quatern. Sci. Rev. 21: 2085–2097.
Kröhling, D. M. and M. Iriondo. 1999. Upper Quaternary palaeoclimates of the Mar Chiquita area, north Pampa, Argentina. Quatern. Int. 57/58: 149–163.
Ledru, M.-P. 1993. Late Quaternary environmental and climatic changes in central Brazil. Quatern. Res. 39: 90–98.
———, H. Behling, M. Founier, L. Martin, and M. Servant. 1994. Localisation de la Forêt d'*Araucaria* du Brésil au cours de l'Holocene. Implications paléoclimatiques. Compt. Rend. Acad. Sci., Paris, Sci. Vie, 317: 517–521.
——— et al. (+ 5 authors). 2005. Paleoclimate changes during the last 100,000 yr from a record in the Brazilian Atlantic rainforest region and interhemispheric comparison. Quatern. Res. 64: 444–450.
Lorscheitter, M. L. and E. J. Romero. 1985. Palynology of Quaternary sediments of the core T15, Rio Grande Cone, South Atlantic, Brazil. Quatern. S. Amer. Antarc. Penins. 3: 55–92.
Lovejoy, N. R., J. S. Albert, and W. G. R. Crampton. 2006. Miocene marine incursions and marine/freshwater transitions: Evidence from Neotropical fishes. J. S. Amer. Earth Sci. 21: 5–13.
Lowell, T. V. et al. (+ 8 authors). 1995. Interhemispheric correlation of late Pleistocene glacial events. Science 269: 1541–1549.
Lynch-Stieglitz, J. 2004. Hemispheric asynchrony of abrupt climate change. Science 304: 1919–1920.
Makarieva, A., V. G. Gorshkov, and B.-L. Li. 2009. Re-calibrating the snake palaeothermometer. Nature 460: E2–E3.
Makovicky, P. J., S. Apesteguía, and F. L. Agnolín. 2005. The earliest dromaeosaurid theropod from South America. Nature 437: 1007–1011.
Maldonado, A. and C. Villagrán. 2002. Paleoenvironmental changes in the semiarid coast of Chile (~32°S) during the last 6200 cal years inferred from a swamp-forest pollen record. Quatern. Res. 58: 130–138.
Mancini, M. V. et al. (+ 5 authors). 2005. Mid-Holocene climatic variability reconstruction from pollen records (32°–52°S, Argentina). Quatern. Int. 132: 47–59.
Mann, C. C. 2005. Oldest civilization in the Americas revealed. Science 307: 34–35.
Marchant, R. et al. (+ 11 authors). 2001a. A reconstruction of Colombian biomes derived from modern pollen data along an altitude gradient. Rev. Palaeobot. Palynol. 117: 79–92.
——— et al. (+ 11 authors). 2001b. Mid- to late-Holocene pollen-based biome reconstructions for Colombia. Quatern. Sci. Rev. 20: 1289–1308.
——— et al. (+ 12 authors). 2002. Pollen-based biome reconstructions for Colombia at 3000, 6000, 9000, 12,000, 15,000 and 18,000 ^{14}C yr ago: Late Quaternary tropical vegetation dynamics. J. Quatern. Sci. 17: 113–129.
Mark, B. G. and K. F. Helmens. 2005. Reconstruction of glacier equilibrium-line altitudes for the Last Glacial Maximum on the High Plain of Bogotá, Eastern Cordillera, Colombia: Climatic and topographic implications. J. Quatern. Sci. 20: 789–800.
———, G. O. Seltzer, D. T. Rodbell, and A. Y. Goodman. 2002. Rates of deglaciation during the last glaciation and Holocene in the Cordillera Vilcanota–Quelccaya ice cap region, southeastern Perú. Quatern. Res. 52: 287–298.
Markgraf, V. 1985. Late Pleistocene faunal extinctions in southern Patagonia. Science 228: 1110–1112.
———. 1991. Late Pleistocene environmental and climatic evolution in southern South America. Bamberger Geogr. Schriften 11: 271–281.
———. 1993. Climatic history of Central and South America since 18,000 yr B.P.: Comparison of pollen records and model simulations. *In:* H. E. Wright Jr. et al. (+ 5 eds.), Global Climates Since the Last Glacial Maximum. University of Minnesota Press, Minneapolis. pp. 357–385.
———, C. Whitlock, and S. Haberle. 2007. Vegetation and fire history during the last 18,000 cal yr B.P. in southern Patagonia: Mallín Pollux, Coyhaique, Province Aisén

(45°41'30" S, 71°50'30" W, 640 m elevation). Palaeogeogr. Palaeoclimatol. Palaeoecol. 254: 492–507.

Maslin, M. 2004. Ecological versus climatic thresholds. Science 306: 2197–2198.

Mauquoy, D. et al. (+ 6 authors). 2004. Late Holocene climatic changes in Tierra del Fuego based on multiproxy analyses of peat deposits. Quatern. Res. 61: 148–158.

Mayle, F. E., R. Burbridge, and T. J. Killeen. 2000. Millennial-scale dynamics of southern Amazonian rain forests. Science 290: 2291–2294.

Mlot, C. 1995. A high glacier opens a view of the Ice Age tropics. Science 269: 32.

Moore, P. D. 2000. Chile refuges. Nature 408: 532–533. [Where did warmth-loving species shelter from the cold during ice ages? Genetic analyses of a coniferous tree in South America provide an unexpected answer.]

Morbelli, M. A. and G. E. Giudice. 2005. Spore wall ultrastructure in Aspleniaceae (Pteridophyta) from north-west Argentina. Rev. Palaeobot. Palynol. 135: 131–143.

Mountain Geoecology of the Andes. 1993. Congress Proc., Mountain Geoecology of the Andes: Resource Management and Sustainable Development (Santiago de Chile, Oct.–Nov., 1991). Mountain Res. Developm. 13: 115–212.

Mpodozis, C. et al. (+ 5 authors). 2005. Late Mesozoic to Paleogene stratigraphy of the Salar de Atacama Basin, Antofagasta, northern Chile: Implications for the tectonic evolution of the Central Andes. Tectonophysics 399: 125–154.

Nature. 2006. Making the paper, Linda Perry. Nature 440: xiii.

Newton, P. 1997. Hot air, big chill. Nature 387: 854. [Field efforts involved in Lonnie Thompson's research on the stratovolcano Sajama (6548 m) in Bolivia.]

Nores, M. 2004. The implications of Tertiary and Quaternary sea level rise events for avian distribution patterns in the lowlands of northern South America. Global Ecol. Biogeogr. 13: 149–161.

Orquera, L. A. 2005. Mid-Holocene littoral adaptation at the southern end of South America. Quatern. Int. 132: 107–115.

Paez, M. M., C. Villagrán, S. Stutz, F. Hinojosa, and R. Villa. 1997. Vegetation and pollen dispersal in the subtropical–temperate climatic transition of Chile and Argentina. Rev. Palaeobot. Palynol. 96: 169–181.

Pares Regali, M. d. S. 1990. Contribución a la palinológia estratigrafíca de la Formación Malargüe, Cretácico Superior, sur de la Provincia de Mendoza, Argentina. Parte 1: Especies terrestres y de aguas continentales. Ameghiniana 27: 289–303.

Parizzi, M. G., M. L. Salgado-Labouriau, and H. C. Kohler. 1998. Genesis and environmental history of Lagoa Santa, southeastern Brazil. The Holocene 8: 311–321.

Porter, S. C. 2001. Snowline depression in the tropics during the last glaciation. Quatern. Sci. Rev. 20: 1067–1091.

Quattrocchio, M. 2006. Palynology and palaeocommunities of the Paleogene of Argentina. Revista Brasil. Paleontol. 9: 101–108.

———, M. A. Martínez, A. Carpinelli Pavisich, and W. Volkheimer. 2006. Early Cretaceous palynostratigraphy, palynofacies and palaeoenvironments of well sections in northeastern Tierra del Fuego, Argentina. Cretaceous Res. 27: 584–602.

———, W. Volkheimer, R. A. Marquillas, and J. A. Salfity. 2005. Palynostratigraphy, palaeobiogeography and evolutionary significance of the late Senonian and early Palaeogene palynofloras of the Salta Group, northern Argentina. Revista Esp. Micropaleontol. 37: 259–272.

Ramage, J. M., J. A. Smith, D. T. Rodbell, and G. O. Seltzer. 2005. Comparing reconstructed Pleistocene equilibrium-line altitudes in the tropical Andes of central Peru. J. Quatern. Sci. 20: 777–788.

Raven, P. H. and D. I Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

——— and ———. 1975. History of the flora and fauna of Latin America. Amer. Sci. 63: 420–429.

Rodbell, D. T. 2000. The Younger Dryas: Cold, cold everywhere? Science 290: 285–286.

Rodriguez, R., A. Mabres, R. Woodman, B. Balsely, and R. Phipps. 1992. Avances sobre estudios dendrocronológicos en la región costera norte del Perú, para obtener un registro pasado del fenómeno El Niño. Extended Abstracts, Paleo–ENSO Records International Symposium (Lima, Peru, 1992). Orstom, Lima, Peru. pp. 275–280.

Roig, F. A. et al. (+ 7 authors). 2001. Climate variability 50,000 years ago in mid-latitude Chile as reconstructed from tree rings. Nature 410: 567–570.

Rossetti, D. de F., P. M. de Toledo, and A. M. Góes. 2005. New geological framework for western Amazonia (Brazil) and implications for biogeography and evolution. Quatern. Res. 63: 78–89.

Rull, V. 1999. Palaeofloristic and palaeovegetational changes across the Paleocene/Eocene boundary in northern South America. Rev. Palaeobot. Palynol. 107: 833–95. [See also Erratum, 2000, Vol. 109, p. 83.]

———. 2003a. Contributions of quantitative ecological methods to the interpretation of stratigraphically homogeneous pre-Quaternary sediments: A palynological example from the Oligocene of Venezuela. Palynology 27: 75–98.

———. 2003b. An illustrated key for the identification of pollen from Pantepui and the Gran Sabana (eastern Venezuelan Guayana). Palynology 27: 99–134.

———. 2004. Biogeografia histórica de las Tierras Altas de Guyana y origen de la biodiversidad Neotropical. Orsis 19: 37–48.

Salgado-Labouriau, M. L. 1997. Late Quaternary palaeoclimate in the savannas of South America. J. Quatern. Sci. 12: 371–379.

——— and L. Villar de Seoane. 1992. Contribución a la flora polínica de los tepuyes. *In:* O. Huber (ed.), Chimantá,

Escudo de Guayana, Venezuela, Un Ensayo Ecológico Tepuyana. Oscar Todtmann Editores, Carácas. pp. 219–264.

Sandweiss, D. H., J. B. Richardson III, E. J. Reitz, H. B. Rollins, and K. A. Maasch. 1996. Geoarchaeological evidence from Peru for a 5000 years B.P. onset of El Niño. Science 273: 1531–1533.

Schrag, D. P., G. Hampt, and D. W. Murray. 1996. Pore fluid constraints on the temperature and oxygen isotope composition of the glacial ocean. Science 272: 1930–1932. [Estimates tropical Atlantic Ocean was 4° C cooler at the LGM.]

Schofield, E. K. and P. A. Colinvaux. 1969. Fossil *Azolla* from the Galápagos Islands. Bull. Torrey Bot. Club 96: 623–628.

Science Magazine, various authors. 2001. Special Issue: Paleoclimate. Science 292: 657–693.

Seltzer, G. O., D. T. Rodbell, and H. E. Wright (eds.). 2003. Late-Quaternary paleoclimates of the southern tropical Andes and adjacent regions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 1–3.

Shackleton, N. 1967. Oxygen isotope analyses and Pleistocene temperatures re-assessed. Nature 215: 15–17.

Sigman, D. M., S. L. Jaccard, and G. H. Haung. 2004. Polar ocean stratification in a cold climate. Nature 428: 59–63. [See also summary by R. Francois, pp. 31–32.]

Simpson, B. B. 1975. Pleistocene changes in the flora of the high tropical Andes. Paleobiology 1: 273–294.

——— and C. A. Todzia. 1990. Patterns and processes in the development of the high Andean flora. Amer. J. Bot. 77: 1419–1432.

Sniderman, J. M. K. 2009. Biased reptilian palaeothermometer? Nature 460: E1–E2.

Solé de Porta, N. 1972. Contribución a la palinología del nivel de lutitas y arenas (Campaniense) en Guataquí (Valle del Magdalena), Colombia. Revista Esp. Micropaleontol. 4: 225–250.

Stahl, P. W. 2004. Greater expectations. Nature 432: 561–563. [Mid-Holocene (4190 ^{14}C yrs B.P.) archeology, Uruguay.]

Stansell, N. D. et al. (+ 5 authors). 2005. Late Quaternary deglacial history of the Mérida Andes, Venezuela. J. Quatern. Sci. 20: 801–812.

Stevaux, J. C. 2000. Climatic events during the late Pleistocene and Holocene in the Upper Paraná River: Correlation with NE Argentina and south-central Brazil. Quatern. Int. 72: 73–85.

Suguio, K. and D. Mussa. 1978. Madeiras fósseis dos aluviões antigos do Rio Tietê, São Paulo. Bol. Inst. Geoci. Univ. São Paulo 9: 25–45.

Tapia, P. M., S. C. Fritz, P. A. Baker, G. O. Seltzer, and R. B. Dunbar. 2003. A late Quaternary diatom record of tropical climatic history from Lake Titicaca (Peru and Bolivia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 194: 139–164.

Taylor, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and Early Tertiary of the North American area. Bot. Rev. 56: 279–416.

———. 1991. Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Paleocene age. Palaeogeogr. Palaeoclimatol. Palaeoecol. 88: 69–84.

———. 1995. Cretaceous to Tertiary geologic and angiosperm paleobiogeographic history of the Andes. *In:* S. P. Churchill, H. Balslev, E. Ferero, and J. L. Luteyn (eds.), Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden, Bronx. pp. 3–9.

Tellería, M. C. and L. Katinas. 2004. A comparative palynologic study of *Chaetanthera* (Asteraceae, Mutisieae) and allied genera. Syst. Bot. 29: 752–773.

Thompson, L. G. 2000. Ice core evidence for climate change in the tropics: Implications for our future. Quatern. Sci. Rev. 19: 19–35.

———, E. Mosley-Thompson, W. Dansgaard, and P. M. Grootes. 1986. The Little Ice Age as recorded in the stratigraphy of the tropical Quelccaya ice cap. Science 203: 361–364.

van der Hammen, T., J. H. Werner, and H. van Dommelen. 1973. Palynological record of the upheaval of the Northern Andes: A study of the Pliocene and lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its high-Andean biota. Rev. Palaeobot. Palynol. 16: 1–122.

Vélez, M. I., J. C. Berrío, H. Hooghiemstra, S. Metcalfe, and R. Marchant. 2005. Palaeoenvironmental changes during the last 8590 calibrated yr (7800 radiocarbon yr) in the dry forest ecosystem of the Patía Valley, southern Colombian Andes: A multiproxy approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 216: 279–302.

——— et al. (+ 5 authors). 2001. Late Holocene environmental history of southern Chocó region, Pacific Colombia; sediment, diatom and pollen analysis of core El Caimito. Palaeogeogr. Palaeoclimatol. Palaeoecol. 173: 197–214.

Villagrán, C. M. 1990. Glacial climates and their effects on the history of the vegetation of Chile: A synthesis based on palynological evidence from Isla de Chiloé. Rev. Palaeobot. Palynol. 65: 17–24.

———. 1995. Quaternary history of the Mediterranean vegetation of Chile. *In:* M. T. Kalin Arroyo, P. H. Zedler, and M. D. Fox (eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Ecological Studies 18. Springer Verlag, Berlin. pp. 3–20.

——— and L. F. Hinojosa. 2005. Esquema biogeográfico de Chile. *In:* J. L. Bousquets and J. J. Morrone (eds.), Regionalización Biogeográfica en Iberoamérica y Tópicos Afines. Ediciones Universidad Nacional Autónoma de México, México, D.F. pp. 551–577.

Villalba, R., R. D. D'Arrigo, E. R. Cook, G. C. Jacoby, and G. Wiles. 2001. Decadal-scale climatic variability along the extratropical western coast of the Americas: Evidence from tree-ring records. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 155–172.

Vizcaíno, S. F., R. A. Fariña, M. A. Zárate, M. S. Bargo, and P. Schultz. 2004. Palaeoecological implications of the mid-Pliocene faunal turnover in the pampean region (Argentina). Palaeogeogr. Palaeoclimatol. Palaeoecol. 213: 101–113.

Webb, R. S., D. H. Rind, S. J. Lehman, R. J. Healy, and D. Sigman. 1997. Influence of ocean heat transport on the climate of the Last Glacial Maximum. Nature 385: 695–699. [Simulations provide a mechanism for cooling the tropics by 5°–6° C at the LGM.]

Weng, C., M. B. Bush, and A. J. Chepstow-Lusty. 2004. Holocene changes of Andean alder (*Alnus acuminata*) in highland Ecuador and Peru. J. Quatern. Sci. 19: 685–691.

Willis, K. J., L. Gillson, and S. Knapp (eds.). 2007. Biodiversity hotspots through time: Using the past to manage the future. Philos. Trans., Ser. B 362: 166–333.

Winchester, V. and S. Harrison. 2000. Dendrochronology and lichenometry: Colonization, growth rates and dating of geomorphological events on the east side of the north Patagonian icefield, Chile. Geomorphology 34: 181–194.

Wing, S. et al. (+ 5 authors). 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of neotropical rainforest. Proc. Natl. Acad. Sci. U.S.A. 106: 18627–18632.

Ybert, J.-P. 1988. Apports de la palynologie á la connaissance de l'histoire du Lac Titicaca (Bolivie–Pérou) au cours du Quaternaire recent. Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry 25: 139–150.

Zárate, M. A. and J. L. Fasano. 1989. The Plio–Pleistocene record of the central eastern pampas, Buenos Aires Province, Argentina: The Chapadmalal case study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 72: 27–52.

Zhou, M. and C. J. Heusser. 1996. Late-glacial palynology of the Myrtaceae of southern Chile. Rev. Palaeobot. Palynol. 91: 283–315.

SECTION III

SYNTHESES

Chapter 8

THE BROADER PICTURE

Within the past few decades, considerable information has appeared on the geology and climatology of Latin America. This has generated new models describing land-sea relationships, mountain uplift, and environmental change (Background, Chapters 1–3). To effectively utilize these models in a history of the vegetation, however, the morass of paleobotanical information has to be assembled, evaluated, and organized into a manageable format. A beginning of that process is presented in Chapters 4–7 (Database) and in Appendix 2. From these compilations, it is possible to consider events that have taken place over time and across the landscapes of Latin America and to consider their biotic consequences. The processes, events, and responses include closure of the Isthmus of Panama; the origin of the northern temperate element in the Latin American biota; warm intervals and their implications for plant migration; dry intervals and arid corridors; vicariance and dispersal as mechanisms for speciation and distribution; fossils and molecules in biogeography; the history of selected lineages; the stability of tropical ecosystems; and the multifaceted origins of biodiversity (e.g., the role of refugia). The new information supports some older concepts, while requiring others to be modified or discarded from the lexicon of biogeography. The result is a slowly improving understanding of Latin American vegetation as part of an evolving global ecosystem.

CLOSURE OF THE ISTHMUS OF PANAMA AND THE BIOTIC CONSEQUENCES

In the older biogeographic literature, two concepts worked against achieving an accurate view of how present-day spatial patterns were attained. One was the belief that continents and land bridges were fixed in position and that once a lineage had evolved the only means of migration was by dispersal, that is, through the movement of the organisms. For example, in accounting for the origin of the Antillean and Central American fauna, Darlington (1964; see also 1938, 1948, 1957) proposed "centers of origin" (mostly Asian) from which organisms radiated across continents that were permanently located: "The existing pattern has evidently been formed by very complex movements of animals over the world approximately as it is now, not over extraordinary land bridges or drifting continents." (For a review of this and other early biogeographic theories, see Nelson & Ladiges [2001].)

At the other extreme was the view that continents could be moved and interconnected with abandon to account for perceived biological affinities between remote regions. Many of these connections later proved to be geophysically impossible and, during their proposed existence, were taxonomically selective and unidirectional and appeared and disappeared depending on the taxon under consideration:

> "The presence of teeth of *Hipparion*, an ungulate related to the horse, in Europe and South Carolina–Florida prompted French geologist Leoncé Joleaud to propose a land bridge extending from Florida through the Antilles to North Africa and Spain. Subsequently, to accommodate eight new passengers, it was broadened to encompass the entire region from Maryland and Brazil across to France and Morocco and its life was prolonged to include virtually all of the Tertiary. With the later discovery that there were periodicities in similarity between Old World and New World Cenozoic faunas, the continents were envisioned as moving back and forth like an accordion. George Gaylord Simpson [1943], who favored the North Atlantic land bridge to connect North America and Europe, was beside himself with these theories and characterized Joleaud's as 'the climax of all drift theories.'" (I: p. 318)

Udvardy (1969) plotted all the Cretaceous and Tertiary land bridges postulated for the South Pacific up to 1913, and he estimated that the water displaced would have virtually eliminated the Earth's terrestrial habitats.

Other considerations are now recognized as essential for tracing the origin of distribution patterns, in addition to properly positioned continents and land bridges. These include an accurate taxonomy and phylogeny of the organisms under study, and a knowledge of the age of the connection(s) compared to the age and place of origin of the lineage migrating across it. It is useful to know the regional paleoclimates, the time and direction of climatic change, the ecological tolerances of the organism(s), and their dispersal potential. With reference to the Panama land bridge, it is noteworthy that following completion at ~3.5 Ma, the landscape was low-lying and could accommodate tropical migrants, while those requiring more temperate conditions would find a few, widely scattered highlands available only after ~2.5 Ma. In formulating models of land bridge environments, the modification of regional climates from alteration in ocean circulation by the emerging bridge itself is a factor, and during uplift a change in precipitation occurs to create a wetter windward and a drier leeward side. There is always the possibility that organisms with the

Figure 8.1. Looking out to the Pacific Ocean across a mangrove swamp, Ocú–David road, Panama. The setting is reminiscent of the islands and land fragments that occupied the isthmian region during most of the Tertiary period until ~3.5 Ma.

capacity for long-distance dispersal can transgress the barrier at any time, and the probabilities of such events vary with the changing positions of the continents. Rarely, if ever, is all the necessary information known for a region, species, or vegetation type. What is accomplished by assembling the data is that it identifies opportunities and it allows specialists familiar with the distribution potential and ecology of the taxon to estimate the probabilities of migration over a particular pathway. If certain routes appear to have been repeatedly used, they may be hypothesized as available for organisms with lesser-known histories.

The physical history of the isthmian connection has been summarized in Chapter 2, and an impression of the landscape for most of the Tertiary, with bits and pieces of land fragments moving through the region, is shown in Fig. 8.1. Some of these fragments became appressed to the western coastlines as exotic terranes such as the Nicoya, Osa, Burica, and Azuero peninsulas of Costa Rica and Panama. The final overland segment completed through Panama was in the present Darién region between ~3.7 and 3.2 Ma. By ~2.5 Ma, uplands were in existence, a few scattered ± temperate habitats became available, and the differentiation between the present wetter Atlantic and drier Pacific side had begun.

This scenario provides the physical context within which the record of other organisms has been extensively reviewed. The migrations of mammals across the region follow the expectations of the above landscape reconstructions (Stehli & Webb, 1985; Webb & Rancy, 1996; Webb, 1997, 2006). Through the Miocene, affinities of the Central American fauna, other than easily dispersed taxa, are predominantly with North America. In the Pliocene, similarities with South America increase, and late in the Pliocene and especially in the Quaternary, components typical of temperate and drier savanna habitats appear. More mammals moved from north to south than in the reverse direction, and those reaching South America underwent greater diversification. For example, there are now more than 200 genera and 400 species of mice and rat sigmodontine rodents of North American origin representing ~25% of the South American mammal species (Flannery, 2001). South America has more kinds of canines than any other continent, and it has more than half of the world's camelids. Altogether, ~53% of the modern South American mammal fauna is derived from North American ancestors, while only about 10% of North American mammals have South American ancestors (Webb, 1991). Moving into South America were raccoons, bats, shrews, hares, pocket mice, pocket gophers, squirrels, field mice, snapping turtles, cats, saber-toothed tigers, pumas, panthers, weasels, skunks, otters, foxes, wolves, bears, elephantids, tapirs, horses, peccaries, Camelidae, and deer. Moving from south to north were armadillos, sloths, porcupines, capybaras, and opossums.

Table 8.1. Similarity values for Cenozoic palynofloras of southern Central America and northern South America.

	Calculation 1	Simpson's Faunal Index	Sorensen Index
Quaternary	15.7	31.1	21.6
Middle Pliocene	8.9	17.7	15.0
Early Miocene	10.7	19.5	18.0
Middle to late Eocene	2.6	8.9	4.0

The plant fossil record for Central America is summarized in Chapter 6 and cataloged in Table 6.1 and Appendices 2.1 and 2.2. Palynofloras of Eocene to Quaternary age on either side of the isthmus have been compared (Graham, 1992a), and the degree of similarity estimated by three statistical tests:

1. a commonly used unnamed calculation

$$\% = \frac{a}{b + (c - a)} \times 100$$

where a = number of entities in common, b = total number of entities in the first population, and c = total number of entities in the second population;

2. the Sorensen Index

$$\% = \frac{2a}{(2a + b + c)} \times 100$$

where a = number of entities in common, b = total number of entities found only in the first population, and c = total number of entities found only in the second population; and

3. the Simpson Faunal Index

$$\% = (c/n) \times 100$$

where c = number of entities in common, and n = total number of entities in the smaller population. The results are shown in Table 8.1. Using calculation 1 as an example, the similarity value for the Eocene is 2.6%, 8.9% for the Pliocene, and 15.7% (now 29.7%) for the Quaternary. At the time of this study, the Limón Group (formerly Uscari Sequence) was considered early Miocene in age (Graham, 1987), but the megafossils (Berry, 1921) and the microfossils actually came from the overlying Río Banano Formation now dated at 2.4–3.5 Ma (middle Pliocene; see Graham & Dilcher, 1998).

> "What this means for Table 1 [in Burnham & Graham, 1999] is that Graham's indices of similarity between Central America and South America increase gradually from Eocene to Quaternary, making for an even nicer pattern." (Laurel Collins, pers. comm. to Robyn Burnham, 1994)

That is, the values for the Lower Miocene decrease slightly, and those for the middle Pliocene increase. The trend also holds true if the study by Jaramillo and Dilcher (2001) on the Paleogene of Colombia, with its extensive list of carefully documented palynomorphs, is included because the relationships of that flora, other than morphologically generalized forms of broad biological affinities, are primarily with other South American Paleogene assemblages. It is evident from the analysis that the similarity between regions on either side of the isthmus becomes substantially greater after ~3.5 Ma.

The correspondence between the geological, geochemical (Chapter 2), and paleontological evidence for closure of the Isthmus of Panama is impressive but, as expected in such complex, multifactored systems, not all data are congruent. For example, Webb and Rancy (1996) emphasize drier savanna habitats to accommodate browsers and grazers in the Pliocene and Quaternary faunas. There are no Pliocene floras known for Panama (the Gatún flora listed as Pliocene in Graham [1991a, b, c] is now late Miocene). However, in the Pliocene Río Banano flora of Costa Rica (Graham & Dilcher, 1998), the Herrería flora of Guatemala (Graham, 1998), the late Miocene Gatún flora of Panama, and the Quaternary assemblages from Panama (Bartlett & Barghoorn, 1973), pollen of grass and savanna shrubs is scarce or absent, and the assemblage is mostly one of forest trees and shrubs. One factor in the undoubtedly complex explanation for the different vegetation implied by the faunal and paleobotanical evidence is that volcanism likely created a mosaic of local, temporary, shifting, open habitats within the forested environment that supported mobile herds of browsers and grazers (I: p. 100). Another is that drier habitats were developing on the Pacific side of the isthmus in the Pliocene with elevation of the highlands. Together, these factors at least partly account for a fauna with dry savanna-inhabiting elements existing in a region with extensive forests.

A more challenging problem is to explain why such different numbers of plant versus animal species moved in opposite directions across the Panama land bridge, and the reasons for their different rates of diversification after arriving on the respective continents (Burnham & Graham, 1999). In contrast to the animal groups, relatively few trees and shrubs moved from the north into South America (*Alnus*, *Populus*, *Quercus*, *Salix*, *Juglans*), and most of those that did underwent comparatively little speciation (see Erkens et al. [2007] for a tropical rain forest tree [*Guatteria*, Annonaceae] cited as having undergone rapid diversification after a north to south introduction). However, the trees and shrubs that crossed from the south into North America diversified extensively. Recall that 75% of the canopy trees in the rain forests of Mexico have South

Figure 8.2. Localities of Tertiary microfossil floras used to assess the general north-south movement of northern temperate elements into the Latin America biota. From Graham (1999). Used with permission of Oxford University Press, Oxford, U.K.

American affinities (Chapter 4, Paraje Solo flora). Quantitative explanations for such processes are difficult to formulate, but in a narrative construct two factors seem apparent. One is that many of the trees and shrubs moving north to south were temperate elements restricted by the few scattered habitats along the migration route and in the rising Northern Andes Mountains. By contrast, those tropical elements moving from the south, after encountering a narrow filter zone in the isthmus, entered a relatively expansive tropical environment. A related factor is the different configuration of the continents on either side of the isthmus as discussed by Flannery (2001). North America is ~25% larger than South America, and its "virtual size" is increased even further by periodic connection to Asia and Eurasia via Beringia and the North Atlantic land bridge. Conversely, South America was an island continent for much of the Cenozoic. Under the rubric that "size matters," since the Pliocene, diversity of the North American land mammal fauna has exceeded that of South America by ~60%, and this would have favored movement of more kinds of animals from north to south upon completion of the isthmian connection. Their arrival caused some displacement, competition, and extinction in the older mammalian fauna, affecting the present-day numerical representations. Climate changes were more intense over a broader area toward the north, generating greater pressure for southward migration, and the earlier arrival in the north of greater numbers of humans directly or indirectly increased extinctions of the larger mammals, including those from South America. These factors contributed to the complex reverse pattern evident in both the ancient and the

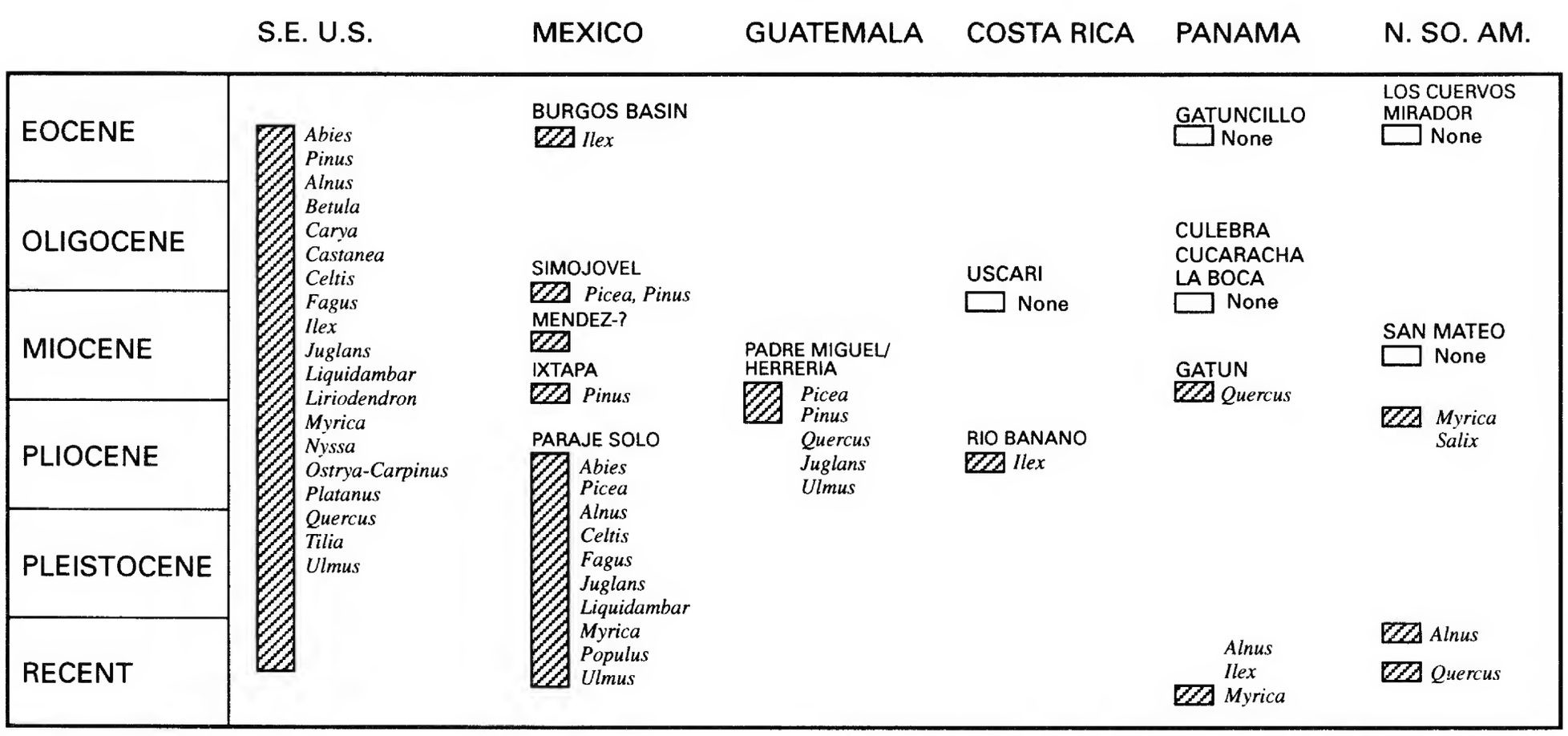


Figure 8.3. Age and distribution of fossil pollen of north-temperate trees and shrubs in Cenozoic sediments of the Gulf–Caribbean region. Note the greater abundance earlier of these elements in the north, and their lesser abundance later toward the south. From Graham (1999). Used with permission of Oxford University Press, Oxford, U.K.

extant biota by differentially affecting the plants and animals on each side of the isthmus.

ORIGIN OF THE NORTHERN TEMPERATE ELEMENT IN THE LATIN AMERICAN BIOTA

The presence of northern temperate plants in tropical and subtropical zones to the south could have originated through one or more mechanisms: (1) ecological differentiation into temperate species in the Neogene from warm-temperate to subtropical Late Cretaceous and early Paleogene ancestors long present and widespread in North and Central America, (2) progressive introduction from the north as climates cooled in the Middle and Late Tertiary and highlands became more extensive, and (3) abrupt long-distance dispersal anytime during the Cenozoic. Axelrod (1975, p. 280), writing when relevant paleobotanical information for northern Latin America was meager, favored the first explanation: "The temperate 'Appalachian disjuncts' in southern Mexico are therefore ancient, and did not migrate south to enter a forest previously without deciduous hardwoods, as others maintain." More precisely defined, the question is not whether the forests of northern Latin America are without deciduous hardwoods; they contain many warm-temperate species that are deciduous by virtue of seasonality in rainfall (e.g., *Alfaroa*, *Clethra*, *Meliosma*, *Oreomunnea*, *Pithecellobium*, *Psychotria*, *Ticodendron*, *Trigonobalanus*, *Weinmannia*). The question is whether those deciduous elements with northern affinities (e.g., *Abies*, *Acer*, *Alnus*, *Carpinus*, *Cornus*, *Diospyros*, *Fagus*, *Juglans*, *Liquidambar*, *Nyssa*, *Ostrya*, *Picea*, *Pinus*, *Platanus*, *Populus*, *Prunus*, *Quercus*, *Salix*, *Tilia*, and *Ulmus*) were mostly present since Cretaceous and Paleogene times, or were mostly introduced later in response to environmental changes of the Middle and Late Tertiary (Graham, 1973, 1999).

The locations of fossil floras of Tertiary age in northern Latin America, described since Axelrod's (1975) paper, are shown in Fig. 8.2, and the northern temperate elements present in these floras, arranged from north to south and from oldest (Eocene) to youngest (Pleistocene, Recent), are shown in Fig. 8.3. The earliest assemblages with the greatest diversity (19 genera) are found in Paleogene to Miocene floras of the southeastern United States. They occur in decreasing diversity and later in time to the south, with 10 genera present in the middle Pliocene Paraje Solo Formation of southeastern Mexico (the same trend holds if the Oligocene Pie de Vaca flora is included, from which paleobotanical information is just becoming available). Five genera occur in the Mio–Pliocene Padre Miguel–Herrería floras of Guatemala, *Quercus* first appears in limited percentages in the palynofloras of Panama in the late Miocene Gatún flora, *Alnus* entered the highlands of Colombia ~1 Ma, and *Quercus* did not appear there until 330 Kyr (Hooghiemstra, 1984, 1989, 1994; Hooghiemstra & Sarmiento, 1991; Hooghiemstra & Ran, 1994).

The paleobotanical evidence suggests a general progressive introduction of northern temperate elements into the south during the Cenozoic. Greater confidence could be placed in the pattern, however, if independent evidence provided a causal mechanism. The fossil floras and the northern temperate genera are plotted on the paleotemperature curve shown in Fig. 8.4. Global temperatures dropped at the end of the early Eocene, then continued at or just above glacial conditions throughout the Oligocene. Sea ice first appears along the margin of Antarctica in the Eocene, significant and permanent ice sheets appear at the Eocene–Oligocene boundary (~34 Ma;

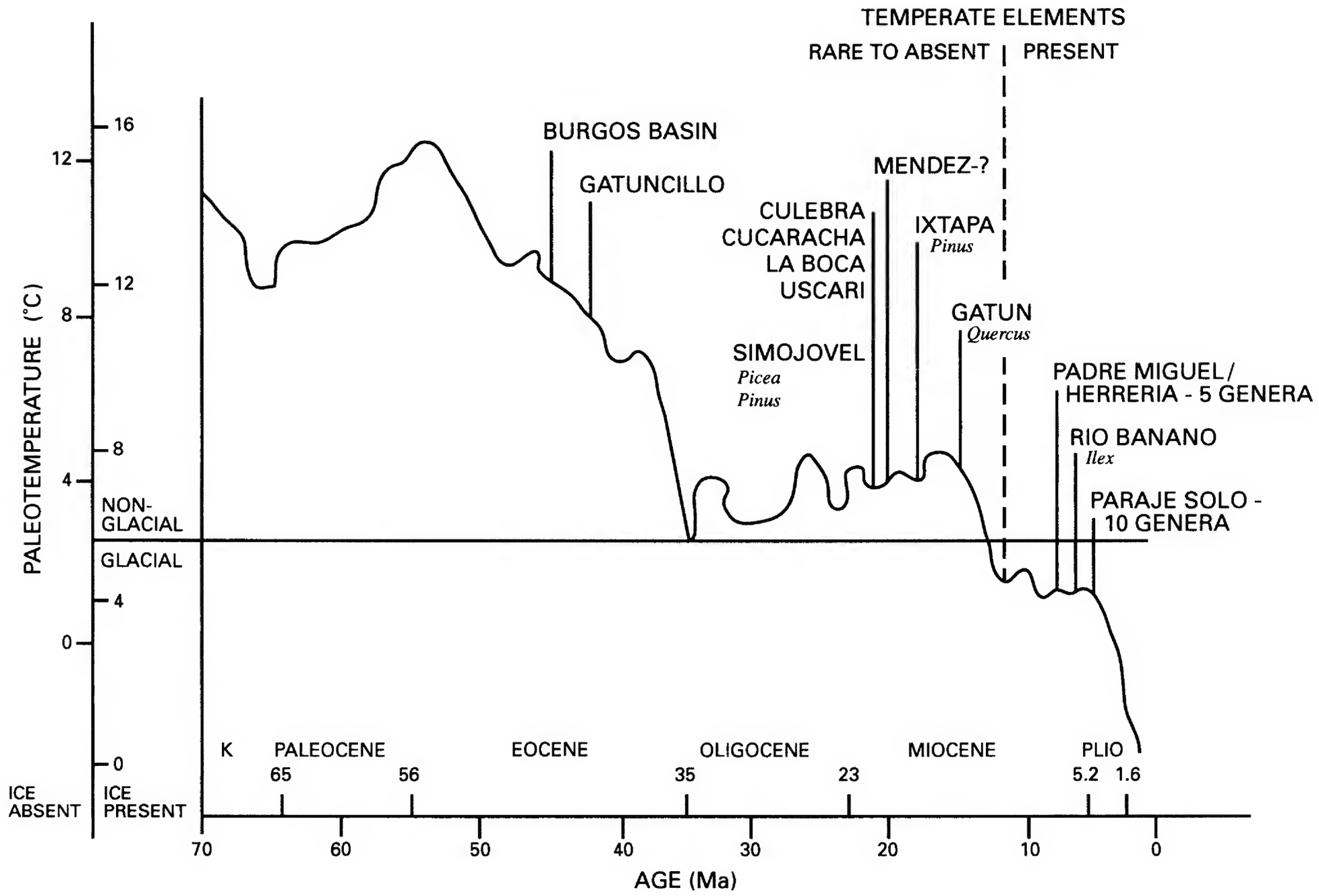


Figure 8.4. Paleotemperature curve (after Miller et al., 1987) with Tertiary palynofloras showing the increase in northern temperate elements after the middle Miocene temperature decline. After Graham (1999). Used with permission of Oxford University Press, Oxford, U.K.

Coxall et al., 2005), and there was a major drop in sea level in the Oligocene ~30 Ma, marking formation of continental ice, full separation of South America from Antarctica through the Drake Passage, development of the thermally isolating circum-Antarctic Current, and the beginnings of the Humboldt Current. Only a few fossils of northern temperate trees and shrubs have been found from this period in northern Latin America. At the end of the early Miocene, another drop in temperature occurred that continued these processes and expanded Early Glacial conditions in the Arctic region and greater seasonality in climates through further ocean cooling. Temperate elements of northern affinity increase significantly at this time in northern Latin America, and they are found farther to the south, until warm temperatures, low-lying landscapes, and the Panama sea barrier reduced or prevented further migration into South America until the late Pliocene–Pleistocene. The paleobotanical evidence now available favors progressive introduction from the north as a means by which many northern temperate elements reached the tropical latitudes.

A related proposal that now can be edited out of the biogeographic literature was that the affinities between the deciduous forests of eastern United States and eastern Mexico date from the Pleistocene (Deevey, 1949). This has been discussed elsewhere (Chapter 4; I: pp. 284–287, 324–327; Graham, 1973, 1976a, b), and unless it is molecularly defined extant lineages that are being considered (see below), suffice it to note that a diverse assemblage of northern temperate elements was already established in eastern Mexico by at least the middle Pliocene (Paraje Solo flora; Graham, 1976a; see examples among Figs. 4.13–4.33; Mio–Pliocene in Guatemala; Graham, 1998).

The periodic introduction of these elements by abrupt long-distance dispersal is also a possibility. However, if this were the primary means of introduction, it would override the pattern of gradual introduction from the north and a significant increase after the middle Miocene cooling event.

PALEOVEGETATION AND PALEOGENE TEMPERATURES OF EQUATORIAL WATERS

In the early days of $^{18}O/^{16}O$-based estimates of marine temperatures, the figures were uncertain because of an unresolved problem. When water evaporates from the ocean surface, more of the lighter ^{16}O is distilled, but under non-glacial conditions it is returned to the marine basins by rainfall and runoff, circulated by currents, and the isotopic balance of ocean waters is maintained (I: pp. 37–40). Thus, when a change in the ratio is observed in the shells of marine invertebrates along DSDP–ODP cores, it can be attributed to fluctuations in water

temperature (an increase in ^{18}O indicates cooling). However, under glacial conditions, ^{16}O-enriched water is retained in the ice and the proportion of ^{18}O in the marine realm increases. If glaciers are known to have been present during a particular interval, compensation can be made for the imbalance. If there is controversy about the presence of glaciers, and there has been for the Paleogene, different estimates will be made of the temperature. This is why two scales are typically presented on paleotemperature diagrams: one for modern (glaciers present) and another for ice-free conditions (e.g., Figs. 4.3, 5.2, 6.2).

The range in estimates of sea surface temperature (SST) for the Paleogene is from ~18°–20° C, assuming an ice-free earth, to ~28° C, assuming the presence of glaciers. Equatorial SSTs are presently ~28° C, so the first estimate would mean that temperatures were lower by 8°–10° C in the Paleogene, and the second suggests they were at least as warm as at present. Terrestrial MATs are estimated to have risen by ~8° C (see Morton, 2005a, p. 1320). This is relevant to interpretations of vegetation history as shown by Axelrod's (1984, p. 128) proposed changes in the ecology of mangroves to accommodate their growth in presumably colder climates. There are also implications for these estimates beyond their importance for vegetational history. The differential between equatorial and high-latitude marine temperatures is one factor that determines the global transfer of heat, and the warm conditions of the polar latitudes in the LPTM and EECL would be difficult to explain if equatorial waters were significantly cooler. Birkenmajer (1990) found glacial deposits in the Eocene of the South Shetland Islands, and Adams et al. (1990) concluded from a review of the distributions of mangroves, reef corals, and larger foraminifera that Eocene SSTs in the tropics were as warm or warmer than at present. This demonstrates some temperature difference between polar and equatorial waters even in the Eocene. A factor in the overall increase in the LPTM–EECL was the release of ~2000 × 10^9 metric tons of carbon in the form of methane. The rapid shoaling (shallowing) of the CCD over a period of <10 Kyr, followed by a gradual recovery (>100 Kyr), dates the event at the Paleocene–Eocene boundary (Zachos et al., 2005).

A sufficient number of Paleogene floras deposited at the continental-marine interface are known to allow an assessment of warm versus cool equatorial temperatures based on paleobotanical evidence (Graham, 1994). These floras are the Laredo (Texas; Gee, 1990, 1992; Westgate & Gee, 1990), Chapelton (Jamaica), Gatuncillo (Panama), and the Los Cuervos and Mirador (Colombia; González-Guzmán, 1967). The Laredo assemblage is presently inland, but in the Eocene it was coastal as evident by the presence of sharks, skates, rays, *Tarpon*, and Crocodylidae, and the Eocene Gatuncillo flora of Panama was fringed seaward by coral reefs. Among the plants present in these floras are *Nypa* (presently an Old World tropical mangrove palm), two other mangroves (*Pelliceria*, *Rhizophora*), and a wide array of taxa that individually, and especially collectively, reflect warm, tropical conditions—*Ceratopteris*, *Coccoloba*, *Combretum–Terminalia*, *Crudia*, *Eugenia–Myrcia*, *Faramea*, *Ficus*, *Mortoniodendron*, numerous palms, *Pteris*, and others. Using *Rhizophora* as an example, its primary northern limit in the New World at present is central peninsular Florida (~26°N), it cannot withstand frost for even brief intervals, and it is clearly associated with SSTs of 27° C or warmer. Thus, the paleobotanical evidence supports the view of warm equatorial waters during the Paleogene. In turn, such interpretations of vegetational history benefit considerably from the context provided by the $^{18}O/^{16}O$ paleotemperature analyses.

DUST, HURRICANES, AND LATIN AMERICAN–AFRICAN PLANT AFFINITIES

> "There is an air bridge that spans the great oceans, and we haven't been paying much attention to it." (Griffin et al., 2002, p. 235)

The ecosystem approach as defined in this text posits that if past and present events, revealed from a wide array of disciplines, are seamlessly integrated into the study of modern vegetation, paleoenvironments, vegetation history, and the origin of lineages and biogeographic patterns, a better understanding of each is likely to emerge. One example involves the increasing number of organisms being recognized in the past and present assemblages of Latin America with affinities to Africa (Guillaumet, 1989; Herngreen & Duenas Jiménez, 1990; George & Lavocat, 1993; Goldblatt, 1993; Hammel & Zamora, 1993; Romero, 1993; Servant et al., 1993; Wyss et al., 1993). The Dominican amber discussed in Chapter 2 has a spectral pattern more similar to the African *Hymenaea verrucosa* than to the New World *H. courbaril* (Hueber & Langenheim, 1986), and the American Lythraceae genera *Crenea* and *Ginoria* have African origins (S. Graham, 2002; S. Graham et al., 2005).

Three means of interchange were available to organisms having African–South American affinities. One was vicariance as South America completed its separation from Africa ~90 Ma. The second was overland migration along the margins of the Tethys Sea, across the North Atlantic land bridge, and into the Americas. This connection was mostly available prior to the middle Eocene, after which physical separations disrupted the bridge and cooling climates filtered migrants with tropical to warm-temperate requirements. Its use is difficult to assess for many taxa because of the paucity of Tertiary floras along major sections of the route (e.g., in northeastern North America). The third means is by long-distance disperal across the developing Atlantic Ocean. Several criteria are important for discerning the most probable mode(s) and pathways of arrival. They include the dispersal potential of the propagules (e.g., viability in sea water, capacity for airborne dispersal, palatability and adhesion to migratory birds, occurrence of the taxon along the migratory route, seed set at the time of avian migrations); dioecious–heterosporous or monoecious–homosporous organisms (the former requiring two simultaneous introductions for subsequent sexual reproduction); general-

ized versus highly specific ecological and edaphic requirements (viz., availability and size of the target area); and a range that includes appropriate directional ocean and atmospheric currents. Historical factors are also important. The North Atlantic land bridge was continuous or nearly so until about the middle Eocene, and climates were warm-temperate to tropical. After the middle Eocene, the route became more discontinuous and conditions trended toward cool- to cold-temperate (I: pp. 60–64). As noted previously, the Central American land bridge with lowland tropical habitats was continuous or nearly so beginning at ~3.5 Ma, but uplands accommodating temperate biotas did not appear until later. Thus, citing the presence of a land bridge to explain a pattern of distribution requires that it also be specified whether the habitat of the organism under consideration is tropical or temperate, coastal or inland, lowland or upland, and if it was likely in existence at the proposed time of migration.

New observations from widely separate fields combine to suggest periods when enhanced dispersal across the Atlantic Ocean after ~90 Ma was favorable for some organisms (Graham, 2005, 2006a, b). It has long been known that impressive amounts of dust are transported each year by hurricanes from the Sahara Desert and the Sahel (the drought-plagued region south of the Sahara of Africa) to the Caribbean region (Gray, 1990; BioBriefs, 1991; Reid et al., 1996; Cadée, 1998; Arimoto, 2001; Harrison et al., 2001; Kohfeld & Harrison, 2001; Prospero, 2001; Prospero & Lamb, 2003; Ryan, 2001; Griffin et al., 2002; Garrison et al., 2003; Toon, 2003; Giles, 2005; Kellogg & Griffin, 2006). Darwin complained that it was dirtying everything on the *Beagle* (Cadée, 1998). In the satellite era, it is possible to quantify the amounts at ~40 million tons/yr of dust, bacteria, diatoms, phytoliths, pollen, fungi, spores, pieces of lichen, and fragments of undetermined affinities (Koren et al., 2006). Interest in the phenomenon has been primarily in its capacity to cause the bleaching of corals, spread of pathogens, and human illness. The potential for the transport of spores, small seeds, and reproductive fragments is obvious but remote given the present distances involved (seeds are not included in the monitoring procedures). However, two other observations, one from the climatological literature and the other from plate tectonics, suggest that at times in the past, and after separation of Latin America from Africa, wind transport of propagules was likely greater than at present.

The first observation is that the intensity, and possibly the frequency, of hurricanes in the Atlantic Ocean has increased significantly in recent years, and the suspected cause is increased energy imparted to the system through global warming (Knutson et al., 1998; Goldenberg et al., 2001; Hoyos et al., 2006; Elsner, 2007). The number of hurricanes has increased twofold over the past six years compared to the previous 24, and major hurricanes have increased 2.5 times (Bengtsson, 2001; Goldenberg et al., 2001; Webster et al., 2005; the Web site http://wind.mit.edu/~emanuel/holem/holem.html explains the thermodynamics of the system). The change corresponds to a rise in temperature of only 0.6° C in the 20th century, and 0.2°–0.3° C in the past 40 years. During the LPTM–EECL (~60–45 Ma), equatorial ocean waters were at least as warm or warmer than at present, mid- to higher-latitude waters were considerably warmer, and bottom water temperatures were 10°–12° C higher (Huber et al., 2000; Schmitz et al., 2000). After a period of temperature decline, there was a rise in the early to middle Miocene (23–12 Ma with a peak between 18 and 14 Ma); in the middle Pliocene (~3.5 Ma), which was the last time the Earth was notably warmer than at present (by ~3.5° C; I: ch. 7; Wrenn et al., 1999); and in previous interglacial MIS 5e. If global warming of 0.2°–0.6° C is presently causing an increase in hurricane frequency and intensity (Schiermeier, 2005), then even warmer intervals in the past should have generated enhanced flow of air from Africa into the Caribbean region and northern South America via the northeast trade winds, possibly from southern South America to Africa via the westerlies, and by the ocean currents they induce.

From the realm of plate tectonics it is known that in the Eocene, the distance between South America and Africa was about one-half to two-thirds that of the present. Furthermore, in the middle to late Eocene, the Greater Antilles began to emerge, and uplift continued through the Cenozoic, increasing target areas for the propagules.

Current molecular studies have not focused specifically on disjunctions at intervals of warmth centered around 55, 18–14, and 3.5 Ma, and the question is whether there is any evidence scattered through the literature for exchange at these times. Davis et al. (2004) suggest that in the Malpighiaceae, six amphi-Atlantic disjunctions occurred from South America to Africa at ~60–31 Ma (middle Paleocene to early Oligocene) and around 17 Ma (early Miocene). Divergence of Neotropical and African *Symphonia* (Clusiaceae) is estimated at 17.36 ± 1.53 Ma (Dick et al., 2003). *Senecio* sect. *Senecio* is considered to have dispersed twice from the Old to the New World (Karin Tremetsberger, pers. comm., 2004), and the main New World lineage is estimated to have become established during the middle Pliocene (3–4 Ma; Coleman et al., 2003). In *Lupinus* long-distance dispersal from the Mediterranean region and Africa to the eastern parts of South America, and independently to North America and the western regions of South America, has been suggested by Käss and Wink (1997). The estimated times are toward the end of the Miocene (~8 Ma) and in the middle Pliocene (~3–4 Ma), respectively. *Hypochaeris* (Asteraceae, Cichorieae) is a genus of ~15 species in the Old World, and >40 species in South America (Tremetsberger et al., 2005, 2006). DNA sequences indicate the South American group originated in northwest Africa and was dispersed to North America 3.5 Ma or less.

New methodologies are opening the possibility of detecting hurricane patterns beyond the time of written records. Heavy rainfall during hurricanes is depleted of the heavier ^{18}O isotope, and this marker is preserved in tree rings. Claudia Mora (cited in Morton, 2005b) has established a record going back several centuries, including evidence for the strong hurricane that hit Cuba in 1780. The announced goal is to extend the

record to 500 years B.P. for use by climatologists in weather predictions. However, the potential exists for detecting events much further back in time; e.g., in fossilized wood from the LPTM–EECL, the middle Miocene climate optimum, the middle Holocene period of global warmth, and the previous warm to warmer interglacials.

The collective evidence combined from different disciplines suggests that opportunities for long-distance transport of propagules were greater for more taxa, over some part of their range, at warm times in the past than would seem plausible under modern conditions. Further studies will demonstrate if there is just coincidence or a real correspondence between times of disjunction and warm intervals, but the observation expands the possibilities for long-distance dispersal to augment transport by vicariance and overland migration.

A SUBHUMID CORRIDOR

At present, there are desert and near-desert, shrubland/chaparral–woodland–savanna, and grassland habitats in central Mexico (the Altiplanicie, the Isthmus of Tehuantepec) and at scattered sites in Central America (the Comayagua Valley of Honduras, the valley of the middle and upper Río Motagua of Guatemala). It has been suggested that these habitats were linked in the Late Tertiary to form a subhumid corridor and that this was the means whereby dry elements were introduced and migrated from southern Mexico through Central America (Stuart, 1954). This might imply that a more extensive arid corridor connected other regions of Latin America, but Stuart (1954) did not suggest, for example, a continuous pathway connecting the deserts of North America and the Monte region of Argentina to account for the similarity in dry elements (e.g., *Acacia*, *Caesalpinia*, *Cassia*, *Cercidium*, *Larrea*, *Mimosa*, *Prosopis*). In fact, the extent and the degree of aridity shown by the photographs in Stuart (1954) is likely, in part, a consequence of modern-day overgrazing and disturbance. However, Campbell (1982), studying fossil birds from the late Pleistocene Talara tar seeps in northwestern Peru and La Carolina in southwestern Ecuador, formulated a climatic model suggesting that during dry intervals of the Wisconsin glaciation, a subhumid corridor along the Pacific coast of Colombia may have connected the dry regions of coastal Ecuador and Peru with those of Central America. More casual references to such a connection are also encountered in the literature, and mentioned in presentations.

From the paleobotanical information now assembled for Mexico, Central America, and South America (Tables 4.1, 5.1, 6.1, 7.1, 7.2, 7.6; Appendices 2.1, 2.2), there is no evidence for a continuous subhumid corridor. Rather, pollen of a few dry elements (savanna shrubs, grasses) are found in the Middle and Late Tertiary. These elements coalesced in the Pliocene and especially in the Pleistocene into more extensive arid communities, but always as part of a mosaic with mesic forested vegetation. Arid communities were most extensive during the driest intervals of the glacial–interglacial transitions (Leyden, 1984, 1985). Even then, however, the suggestion of an essentially continuous arid corridor from the deserts of North America through southern Central America into northern and southern South America overextends the paleobotanical evidence. Shorter-distance dispersal and linkage of some dry habitats likely occurred, but long-distance dispersal is still required to explain the interchange of the most widely disjunct desert and near-desert plants between North and South America.

THE MANY FACES OF BIOGEOGRAPHY

> "Anything can be anywhere." (Zack Jenks, fictional book scout in Larry McMurtry's *Cadillac Jack*, 1982, Simon & Schuster, New York, p. 23)

> Biogeography is the science that describes and interprets the geographic distributions of organisms along spatial and temporal scales. (Paraphrased from Avise, 2004; Walter, 2004)

There has been a renaissance in biogeography engendered by the prospects of achieving new insights through molecular and statistical methodologies and by technological innovations (e.g., geographic information systems [GIS]).[1] There is also a practical impetus arising from the need to better understand the distribution of plant and animal pathogens and invasives. The insights resulting from these new technologies build on the rich archive of information in the older literature and complement continuing geological, paleontological, and taxonomic (monographic, floristic) investigations. A focus of this renewed interest is on migrations generally, and vicariance and dispersal in particular, as evident by numerous books (Dingle, 1996; Clobert et al., 2001; Lomolino & Heaney, 2004; Lomolino et al., 2006), symposia (Cain et al., 2003; Renner & Givnish, 2004; Graham, 2005, 2006a; Winkworth & Lohmann, 2005), reviews (Nelson & Ladiges, 2001; Levin et al., 2003; de Queiroz, 2005; *Science*, 2006), forums (Ebach, 2004), and papers (e.g., Malcomber, 2002; Muñoz et al., 2004; Sytsma et al., 2004). Just as some older biogeographic concepts now require reassessment, some current methods, conclusions, and attitudes will undoubtedly provide fodder for future generations of critics. Nonetheless, it is possible to weave through the proclamations, canonizations, and denigrations in some of the literature to see significant improvements in the theory and practice of biogeography.

Dispersal and Vicariance

Dispersal is the movement of organisms over the landscape, and it may be gradual or abrupt via LDD (Higgins et al., 2003). In the latter case, dispersal is also a mechanism for speciation in that organisms carrying portions of the gene pool become isolated from the parent population and follow independent evolutionary pathways. Vicariance is the separation of a population into subpopulations by the intervention of a barrier. It is a means of dispersion if the habitats move apart, and it is a speciating mechanism if taxa cannot cross the barrier. Examples of vicariance include the separation of South America

from Africa; the uplift of the Andes Mountains placing some populations in drier habitats developing to the west and others in the wetter environments to the east; and the development of hyperarid conditions in the northern Gulf of California region, isolating some populations in Baja California and others in mainland Sonoran Mexico. It seems intuitively obvious that both means of dispersion occur and that their relative importance varies with the geological history of the region and with the group being analyzed. The separation of South America from Africa in the Cretaceous is not as relevant to the origin or early dispersion and speciation of the Asteraceae as to more ancient groups, because the family is not clearly documented in the fossil record until the Oligocene (possibly in the Eocene; see Lineages, Asteraceae below). India separated from Africa in the Cretaceous; land discontinuity and cold climates through the North Atlantic began disrupting the movement of tropical elements across that land bridge after the middle Eocene; the Sahara Desert developed in the Miocene, dividing mesic communities into northern and southern populations (Douady et al., 2003); and glaciers, river valleys, and marine inundations subdivided populations in many parts of the world in the Quaternary. However, what may intuitively seem logical, as well as evident from the study of modern organisms and the geologic record, did not stymie enthusiastic promotion of vicariance as the most important, if not the only significant, means by which biogeographic patterns and affinities are established:

> "Vicariance is, therefore, of primary importance in historical biogeography, and dispersal is a secondary phenomenon." (Croizat et al., 1974, p. 278)

> "The best first-order explanation for an observed disjunct distribution between sister groups is that it represents a fragmentation of a widespread ancestral species, rather than a dispersal phenomenon from a more restricted 'center of origin.'" (Wiley, 1988, p. 514)

> Dispersal events have been characterized as haphazard processes resulting from organisms moving restlessly about (Rosen, 1976, p. 431), and dispersal biogeography as a science of the improbable, the rare, the mysterious, and the miraculous. (Nelson, 1978)

The islands of the Caribbean have been a center for studies on vicariance and dispersal (e.g., Rosen, 1976, 1985; see summaries in Graham, 2003a, b, 2005, 2006a, b). One reason was the tectonic history of the Caribbean Basin as described by Malfait and Dinkelman (1972). According to this model, in the Cretaceous and Paleogene, continuous or near-continuous land extended through the isthmian region and connected or nearly connected the North and South American continents. This segment of land subsequently moved relatively eastward and, in the later Paleogene, fragmented into the islands of the Greater Antilles. Such a model provides an ideal physical setting for vicariance and, indeed, some island fragments are now confirmed to have separated, and collided, during the Tertiary (Chapter 2, The Antilles). However, there is a more recent model around which consensus is developing (Pindell, 1994; Pindell & Barrett, 1990). In this case, the land of the isthmian region originated as a volcanic arc of islands that moved relatively eastward and were never continuous and never connected the two continents. This allows a role for dispersal, as well as for vicariance, and this is the view emerging from recent studies (e.g., Givnish & Renner, 2004; Heinicke et al., 2007; Trénel et al., 2007). Also, Jamaica was submerged between the middle Eocene and the late Miocene (Chapter 2, The Antilles), and there is no geological evidence that it was connected to other lands after that time. Thus, the present flora and fauna of Jamaica must have arrived by dispersal and subsequently diversified. In general:

> "…molecular dating of lineage divergences favors oceanic dispersal over tectonic vicariance as an explanation for disjunct distributions in a wide variety of taxa, from frogs to beetles to baobab trees. Other evidence, such as substantial gene flow among island populations of *Anolis* lizards, also indicates unexpectedly high frequencies of oceanic dispersal. The resurrection of oceanic dispersal is the most striking aspect of a major shift in historical biogeography toward a more even balance between vicariance and dispersal explanations. A high frequency of dispersal also suggests that a fundamental methodological assumption of many biogeographical studies—that vicariance is *a priori* a more probable explanation than dispersal—needs to be re-evaluated and perhaps discarded." (de Queiroz, 2005, p. 68)

The key phrase is "a priori a more probable explanation than dispersal." In earlier geologic times (viz., in Cretaceous) and among the higher taxonomic categories (family and some genera), vicariance must have played a prominent role in the distribution of lineages. It can also be important in more recent times and at lower taxonomic levels as physical and ecological barriers develop. The distribution of the southern beech (*Nothofagus*) is an example. It has limited dispersal capacity, and the fossil record puts it at a time (Cretaceous, Paleogene) and place (Australia, New Zealand, South America) when the tectonic history is compatible with vicariance as a means of distribution (see review in Nelson & Ladiges, 2001). Dispersal is an important means of distribution at any time depending on physical features of the landscape and the distribution capabilities of the propagules. It varies in importance with the changing positions of the continents and the formation and modification of barriers, and it is conditioned by the prevailing environment. It is the principal means of distribution in island settings, and was so in later geologic times when the major separation of landmasses had been achieved. One means of assessing the probabilities of dispersal and vicariance is by estimating the

dates of divergence from nucleotide or amino acid sequences for lineages on either side of a barrier and comparing the results with estimates of the age of the barrier. For example, internal transcribed spacer regions in *Adansonia* (baobab tree) yield a broad range in the time of separation for African and Australian populations between 5 and 23 Ma (Baum et al., 1998). Even given the uncertainties of molecular clocks, this is considerably more recent than the separation of the continents beginning at ~120 Ma, and indicates transport across an ocean barrier. Hedges (1996) used molecular evidence to suggest that dispersal over a 60-Ma period accounted for the presence of terrestrial vertebrate lineages in the Caribbean region, rather than ancient vicariance separations. Geographic patterns in plants interpreted as evidence of dispersal are in the Malpighiaceae (Davis et al., 2002), Rapateaceae (Givnish et al., 2000), and Atherospermataceae (Renner et al., 2000). Thus, dispersal over water, dispersal across land connections, and vicariance have been utilized by various plant and animal groups (Iturralde-Vinent & MacPhee, 1999). Paleontology, accurate distributions (Parenti & Humphries, 2004), and molecular studies that compare genetic and geographic distance (Ebach, 2004) are valuable sources of information in reconstructing histories of migration. This synthetic view is now in the ascendancy as reflected by matter-of-fact statements assuming it to be so: "Contemporary patterns of dispersal and gene flow certainly imprint a species with characteristic phylogeographic signatures,[2] but so too can more ancient factors such as population isolations and subsequent patterns of dispersal. The realized molecular phylogeographic structure of almost any species or taxonomic assemblage is likely to reflect some blend…between current and former biogeographic processes" (Avise, 2004, p. 895).

With reference to the roles of morphological and molecular evidence: "Molecular biogeographic reconstructions are almost invariably of greatest interest and utility when interpreted in conjunction with traditional sources of biogeographic inference, such as historical geology, fossil evidence, and organismal phylogenies as derived from morphological or other evidence. The hackneyed 'molecules versus morphology' debate that characterized earlier decades of the molecular revolution in systematics, beginning in the 1960s, should now be relegated to the status of a rather unfortunate footnote in the socio-politics of science" (Avise, 2004, p. 896; see also Stace, 1989; Lomolino et al., 2006, pp. 142–143).

Examples of the beneficial interactions between geology, historical biogeography, and evolution have been presented earlier with reference to Amazonian freshwater fishes (Chapter 2, South America) and speciation in the giant Galápagos tortoise (Chapter 7, Galápagos Islands). It is also evident from studies of rodent populations in the Amazon Basin. Wallace early on proposed that the distribution of mammals in Amazonia is strongly influenced by the major rivers—his riverine hypothesis (Wallace, 1849, 1876). Da Silva and Patton (1993) found this was generally true for the tamarins, but some rodent populations showed a different pattern, one not obvious from morphology but from mtDNA analysis (see also Patton et al., 1994; Gibbons, 1996; Morell, 1996; Patton & Da Silva, 1998, 2005). It was expected that the populations on either side of the Juruá River might be distinct, but in this case it was ones at the upper reaches of the river that were different from those at the mouth, even though there was no apparent barrier between them: "What is really striking…is that all 11 [of the 17 species] are separated at almost the same geographical point on the river, although there is nothing remarkable about the spot—no bend, no hill, no valley" (Patton quoted from Morell, 1996, p. 1497). The reason is a consequence of past geologic events. During the Late Tertiary, uplift of the Andes Mountains created a series of folds and arches that divided the basin into subbasins. Later in the Cenozoic, erosion products from the Brazilian and Guayana highlands and from the Andes Mountains contributed more than 4000 feet of sediment to the basin and obscured the arches. The mostly buried Iquitos Arch cuts across the river at the point where molecular differentiation in the rodent populations is apparent. When the arches formed and while they were emergent, they disrupted distributions and constituted barriers to migration. Some evidence of the effect is still preserved in the molecular signature. Mitochondrial DNA analysis dates the divergence at 1–3 Ma. In addition to structural features like arches, drainage patterns that change through time are another engine of biodiversity for the Amazon Basin (Rossetti et al., 2005). Both are means of periodically fragmenting populations into reproductively isolated segments that favor the generation of new genotypes over models assuming continuous or near-continuous plant formations across the basin.

Thus, the effects of past history are reflected in genomes and provide clues as to the complex origins of these genomes. This was the point in calling attention to the different physical histories of the three regions from Mexico through the Chortis Block of northern Central America, southern Central America, and the Amazon Basin and adjacent uplands (Graham, 1997). In the northern part, uplift of the Transvolcanic Belt during the Cenozoic provided considerable physiographic diversity, continuous land surfaces, and continuous land connections, particularly to the north. The zone also experienced the most intense climatic changes. In the central part, physiographic diversity and climatic impact in the Tertiary was less, the environment was insular, land surfaces were discontinuous with no (or less) land connection to the north and south, and the vegetation was frequently disrupted through extensive ash falls. Within the Amazon Basin and in the uplands immediately surrounding it, the physiography was relatively low-lying and structurally continuous, and climatic change was comparatively muted. Large areas were frequently inundated and drained by tectonic movements and, increasingly toward the end of the Tertiary, affected by sea-level fluctuations. The three areas all had physical environments that were dynamic, but in different ways, and these produced distinct landscape histories. This raises the possibility that populations of some old and widespread genera distributed across these areas might retain pre-

served in geographic sections of their range distinctive morphological, cytological, or genetic traits that were elicited by the different histories. This is the topic addressed more recently by Avise (2004, p. 895) from the standpoint of phylogeography:

> "Of special note were the well-ear-marked phylogeographic subdivisions often observed within particular species. Sometimes referred to as 'evolutionarily significant units' or 'intraspecific phylogroups,' these genetically distinctive and spatially coherent regional assemblages of conspecific populations often appear quite relatable to past biogeographic agents. Collectively, such empirical findings, accumulated for large numbers of species, amply evidence the importance of historical (as well as modern) biogeographic factors in having shaped the genealogical relationships of geographic populations within species"; viz., "salient but formally cryptic historical partitions within various species… ."

The point of taxonomic interest is that if a trait appears associated with geography, it may be the residue of former interactions between geology and genomes. Such examples are not likely to be rampant and obvious, but may be useful in considering the phylogeny of particular lineages.

Cautionary notes and opinions 4 (Narrative biogeography):

In the contentious days of dispersal versus vicariance, the former was characterized, in a negative sense, as narrative biogeography. In my opinion, narrative biogeography is the Holy Grail of the subject. If after utilizing the impressive array of statistical tests available, a cogent description of a biogeographic event or lineage history cannot be verbally enunciated (viz., narrated), it is likely that the quest for the model has become the focus, and that mathematical symbolism is serving as a substitute for real understanding and a cover for things unfamiliar.

RECONCILING BIOGEOGRAPHIC HISTORIES: FOSSILS AND MOLECULAR-DEFINED LINEAGES IN *RHIZOPHORA*

In addition to earlier advocacy of permanence of continents and ocean basins, dispersal from centers of origin as the sole means of migration, and vicariance as the only meaningful way to view the origin of disjuncts as well as molecules versus morphology, another issue that has delayed achieving a better understanding of biogeographic patterns and phylogeny is molecules versus fossils in dating lineages. This is partly due to the quest for an alternative way of reading the past, given the gaps in the fossil record and the fact that paleobotanists have not done a very good job of filtering out misidentifications and databasing verified annotated records. While these larger problems are being addressed, there are opportunities for fine-tuning the interactions between molecular studies and paleobotany to achieve a better perspective of lineage histories.

The mangrove genus *Rhizophora* produces abundant and distinctive pollen, and it has an extensive fossil record (Graham, 1995, 2005, 2006c). The record is unsettled, however, because of unverified identifications in Paleocene through middle Eocene material. According to Muller (1981, p. 62), "The oldest records are still the upper Eocene occurrences of *Zonocostites ramonae* reported by Germeraad, Hopping, and Muller (1968) from the Caribbean area and confirmed by Pares Regali, Uesugui, and Santos (1974a, b) in Brazil." That assessment still holds true. However, the earliest appearances in Southeast Asia and the Caribbean region are close in time, at the beginning of the late Eocene, and there is no conclusive evidence for a New World or Old World origin of the genus.

The history of *Rhizophora* in the New World has been reviewed by Schwarzbach and Ricklefs (2000, 2001) as part of important ongoing studies of the family Rhizophoraceae. One possible reading of the molecular data is that *Rhizophora*, after appearing in the Caribbean region ~45 Ma (based on fossils), could have disappeared, then been re-introduced about 11 Ma, diversifying into the present-day populations. The most likely time for its disappearance would have been near the end of the middle Miocene (~14 Ma), when the late Cenozoic cooling trend was under way and northern temperate elements were being introduced into the northern Latin American biota. If *Rhizophora* did disappear for a period of ~3 Ma between ~14 and 11 Ma, or at any other time, this should be evident because its fossil record in the Caribbean is one of the most extensive in the world due, in part, to its being an important stratigraphic marker widely used in the petroleum industry.

Rhizophora pollen is present in the New World beginning at the base of the upper Eocene. Prior to that time, brackish-water habitats included a plant of unknown biological affinities producing pollen described as *Brevitricolpites variabilis*. After the early Eocene, it disappeared and *Rhizophora* pollen is present in virtually every deposit from lowland coastal environments in amounts ranging up to >90% in some assemblages. There is no evidence for an absence of any significant duration. Hence, evidence from fossils indicates *Rhizophora* has had an essentially continuous presence in the Caribbean region after ~45 Ma.

The difference between the two records is that one is based on the relatively conservative character of pollen morphology and indicates the presence of *Rhizophora*—as a genus—more or less continuously for the past 45 Ma. A similar stasis would likely be reflected in histories based on wood, leaves, fruits, and seeds. The other record is based on molecularly defined extant lineages, calculation of branch lengths, and estimates of molecular divergence assuming that bases of the DNA are mutating at a constant rate or can be statistically adjusted to a constant or near-constant rate (see below). That record indicates that *Rhizophora*—in the sense of molecularly defined present-day lineages—may have appeared in the Caribbean region ~11 Ma. These are not quite the same as phylogenetic stem and crown groups, and it is important that the particular kind of record being discussed is clearly specified because, as

fossil records improve and as molecular studies are completed for more taxa, such seeming disparities will become commonplace. This applies equally to discussions about the origin of floristic affinities between eastern North America, Asia, and Mexico, and the age of *Ephedra* (Rydin et al., 2004) and various other families (e.g., Meliaceae, see below).

NOTES ON SOME LINEAGES

The paleobotanical database presented here for Latin America consists of ~300 floras ranging in age from the Late Cretaceous through the Quaternary (Tables 4.1, 5.1, 6.1, 7.1, 7.2, 7.6; Appendices 2.1, 2.2). About 8000 taxa are included and are distributed among the four geographic regions as follows:

Mexico	~950 taxa
Cretaceous and Paleogene	250
Neogene	275
Quaternary	425
Antilles	550 taxa
Cretaceous and Paleogene	270
Neogene	90
Quaternary	190
Central America	750 taxa
Cretaceous and Paleogene	50
Neogene	325
Quaternary	375
South America	5750 taxa
Cretaceous and Paleogene	3550
Neogene	1550
Quaternary	650

The fossil record of some representative taxa is provided below as examples of the syntheses that can be made from the tables and appendices, the catalogs and electronic databases mentioned in the Prologue and elsewhere in the text, and from collaborations.

Cautionary notes and opinions 5 (Assessing the plant fossil record):

In using the names in the paleobotanical literature, it is worthwhile for the general reader and specialists in other fields to be aware not only of the widely recognized gaps but of the subtleties in the variable reliability of the record. The accuracy of identifications of megafossils in the database is in part a function of when the identifications were made. Those completed in the early decades of the 20th century were often biased toward results from temperate regions of northern North America and Europe; interpretations were less constrained by phylogenetic, ecological, and biogeographic provenance; comparison of megascopic features of modern and fossil material was not based on detailed leaf architecture utilizing a standardized nomenclature (Hickey, 1973, 1979; Leaf Architecture Working Group, 1999); and fruit, seed, and anatomical collections were not extensive. There were no plant microfossil inventories to provide clues or to support identification of the megafossils, and there was considerably less herbarium material. In 1925, collections at US numbered ~1 million specimens, compared to the present 4.5 million, and at MO they were <900,000 compared to the current >6 million specimens. As a result of these factors, about 60% of Berry's identifications from the middle Eocene Wilcox flora of the Mississippi Embayment region are estimated to be incorrect (Dilcher, 1973), and it can only be guessed what the figure is for his and other early authors' studies of Cretaceous and Tertiary floras of Latin America.

Greater confidence can be placed in the reliability of recent identifications from the plant megafossil record because they involve paleomonographic studies of individual lineages that complement paleofloristic studies that deal with entire assemblages. For example, identifications are being established on a taxon-by-taxon basis for such floras as the Pie de Vaca of Mexico (e.g., Magallón-Puebla & Cevallos-Ferriz, 1994), the Azogues of Ecuador (Burnham, 1995), and numerous ones from Argentina (e.g., the Chenque flora; Barreda, 1997a). For the Quaternary, macroscopic assemblages from rodent middens can be compared directly with extant local vegetation in the arid regions of Mexico (Van Devender, 1990) and Chile (Betancourt et al., 2000), and from other kinds of Neogene and Quaternary deposits in Colombia (Wijninga, 1996), Brazil, and Peru (Hoorn, 1994). Increasingly, stratigraphic, paleoenvironmental, phylogenetic, and biogeographic interpretations are being globally integrated and context-based.

For the microfossil record, reliability of identifications is not so much a matter of when the study was done because, compared to megafossil paleobotany, the palynological technique is a relatively recent innovation. Like paleobotany, however, the adequacy of modern comparative material is important. Early palynological work on the Tertiary of Puerto Rico was based on a spore and pollen reference collection of ~10,000 slides, while later studies in Mexico, Guatemala, Costa Rica, Panama, and Bolivia were based on >23,000 slides, numerous catalogs and monographs, and considerably more taxonomic, ecological, and geological information. The value of an extensive vouchered reference collection is twofold. It increases the chances of finding a modern pollen type similar to the fossil specimen and, equally important, it reduces the chances that there are similar types in other taxa. For example, the presence of the Old World tropical genus *Pandanus* in the New World depends on the fossils being similar to the modern pollen of that genus. It also depends on establishing the likelihood that there are no other genera with similar spheroid, monocolpate, or echinate pollen, and this is dependent on the size and completeness of a vouchered reference collection.

In addition to the scope of the collection, the dependability of identifications in the plant microfossil literature reflects the extent to which the stratigraphic, paleoenvironmental, phylogenetic, and biogeographic implications have been taken into account. This, in turn, depends on the intent of the study (stratigraphic or botanical), background of the individual (geological or biological), and how cautiously or how casually biological names and affinities are attributed to

fossil palynomorphs. In general, the biological affinities cited for specimens named by an artificial nomenclature, and used primarily for purposes of stratigraphy, are less important to these studies than those used in primarily biological investigations. However, there are notable exceptions. The botanical affinities and ranges of taxa carefully established over the years by Thomas van der Hammen (e.g., 1961) and his associates for Cenozoic deposits in Colombia and the Guianas, and by Jan Muller (1981; and by Muller in Germeraad et al., 1968) for palynomorphs of the Maracaibo Basin of Venezuela, are valuable contributions both to stratigraphy and to vegetation history. There are many Late Cretaceous and Tertiary microfossil floras in Latin America for which biological affinities have been assigned with care, but overall the record is uneven. For Quaternary palynofloras, identifications are generally accurate, with the exception of some species distinctions and generic identifications attempted within stenopalynous groups. Thus, the task facing systematists and biogeographers utilizing the Late Cretaceous and Cenozoic paleobotanical record in its present state is to be aware of how long ago the study was done (particularly for megafossils) and what was its primary purpose (particularly for microfossils). Current trends are for collaborative investigations (e.g., Manos et al., 2007) and for taxonomic specialists to examine fossils attributed to their group(s). For Latin America, many specimens reported in the older literature are in the Paleobiology Division of the U.S. Natural History Museum (Smithsonian Institution), and these are conveniently housed in the same building as the herbarium. In Latin America, many others are accessible in paleobotanical centers also associated with major museums and herbaria.

Cautionary notes and opinions 6 (Molecular clocks):

Gaps and misidentifications in the fossil record have plagued efforts to adequately date divergences and to achieve consistency between lineages and biogeographic histories suggested by paleobotanical evidence and those emerging from molecular systematics. One way around the problem earlier was to contemplate the possibility of a regularly beating molecular clock (clock-based [Langley-Fitch] age estimates). The clock is not constant, however, and even with improving statistical tests for smoothing out irregularities (clock independent [nonparametric rate smoothing; penalized likelihood]), the dates still are often way too young or too old, have a range too wide to be of use, or do not correspond to reasonably well-documented fossil records (Deep Time Project, 2002 et seq.; Forest et al., 2005; Penny, 2005; Smissen et al., 2005). Nonetheless, when there is a coincidence between clock dates and the fossil record, or where there is no fossil record sufficient to check the dates, it is tempting to adopt the position that they are at least better than nothing.

Examples of difficulties are clock estimates for the age of extant *Ephedra* of 8–32 Ma (Huang & Prince, 2003) when the fossil record goes back 120 Ma or more (Rydin et al., 2004, 2006), and for estimates of divergence of Paleozoic coelacanths ranging between 1.3 and 40 Ma. Phylogenetic studies of the Meliaceae (Muellner et al., 2006) suggested early on an age for *Guarea* of late Oligocene (~30 Ma). A complication was the report of the genus, formerly referred to *Ficus* (Moraceae), in the Late Cretaceous Lance and Hell Creek formations of Wyoming (Graham, 1962). The age of these dinosaur-bearing formations is well established, and specialists "at Kew and abroad (among them Meliaceae and Moraceae morphologists) had a look at the figures in the 1962 paper and confirm that the specimens are not Moraceae, but seem to be indeed the *Guarea* species [to which] you referred the specimens" (Alexandra Muellner, pers. comm., 2005). A recalibration of the *rbcL* phylogeny using the above fossils yielded an equally unlikely preliminary age for the Meliaceae of >240 Ma (early Triassic or older). Anderson et al. (2005) note for the eudicots that "removing one single fossil changes the results in the magnitude of tens of million years." Forest et al. (2005, p. 118) found similar difficulties in reconciling fossil and clock dates in the Betulaceae—"the age of the crown group and stem lineage of Betulaceae vary from 115.2 to 130.6 million years and 211.2–302.6 million years (Aptian or before)" and "only in some cases were molecular- and fossil-based age estimates reconciled."

Many current studies are acknowledging the often unsatisfactory results of calculations based on the assumption of a molecular clock, or on its modifications. Meanwhile, as an alternative, increasing efforts are being made to improve the quality of paleobotanical information available for systematic and biogeographic use. One way is through the detailed studies of the global fossil record of individual lineages as previously mentioned, and then calibrating the clocks and dating nodes using only identifications confirmed by specialists and from well-dated deposits (e.g., see Melastomataceae below, Renner et al., 2001; Juglandaceae, Manos et al., 2007). This reduces the paleobotanical database even further, and the incompleteness of the record still remains, but it minimizes the additional "garbage in, garbage out" effect of uncertain ages and identifications. If the oldest records are ambiguous or not verifiable, one option is to either defer suggesting dates for events because adequate information is not available or discuss these in the context of relative ages. For some, this may have an unsatisfactory feel to it, so another option is to present a range in the estimates of origin, divergence times, and migration events based on (1) all plausible occurrences in the fossil record and (2) on occurrences where the identification and age have been verified.

Another method proposed for establishing the age of at least one node is to use vicariance and assume that divergence dates, for example, from the time South America separated from Africa or from the time the Andes Mountains divided parts of western South America into drier and wetter sectors. In theory, this would provide three means for dating a node—molecular, paleontological, and vicariance—and the dates would be considered probable if there is congruence between at least two of the three approaches. However, each method involves significant uncertainties. In molecular dating,

it is the irregular beat of the clock. For paleontology, it is the incompleteness of the fossil record that remains even after the vagaries of misidentification have been reduced. For vicariance, it is often the transitional nature and broad range of the times involved as continents part and mountains rise. South America began separating from Africa in the south at ~120 Ma and completed separation in the north at ~90 Ma, followed by a long period of gradually increasing distances with intervening islands. During the entire history of the Andes Mountains, valleys transgressed these highlands allowing some east-west migration, especially of drier elements. With geologic events, it is possible to use a range between the beginning and the completion of the process (Conti et al., 2002), comparable to using the first possible and the first confirmed appearance of the taxon in the fossil record.

Ultimately, however, congruence is not being sought between results from an uncertain methodology, an incomplete and inaccurate fossil record, and transitional events that often take millions of years to complete and that are complicated by alternative means of migration. Nor is the goal to have enough fossil records to legitimize use even of an improved molecular clock (Renner, 2005). The goal is to have enough identifications, dates, and congruencies that the clock becomes less important or unnecessary. Congruence is sought between estimates of origin, relationship, and migration based on multigene molecular and morphological studies, and dates based on an adequate fossil record. The number of lineages that qualify are few, but they constitute a reliable template for considering taxa with poorer fossil records. From these lineages, patterns may emerge that identify a place of origin common to many separate taxa (e.g., Lauraceae, west Gondwana), a time of early diversification and radiation (Late Cretaceous), and/or a frequently used pathway of migration (out-of-India; Conti et al., 2002; Rutschmann et al., 2004)—viz., a context provided by deep-time model organisms. This means that for some groups, an accurate time frame for their origin, evolution, and radiation simply may not be available. For these, clearly identified preliminary hypotheses and speculations are a valuable means of organizing and seeking patterns from the data. However, it is the aggravatingly slow accumulation of accurately identified and securely dated fossils that ultimately must provide the basis for establishing specific, absolute (as opposed to relative) divergence and migration times. This is especially so as the reliability/consistency of molecular clocks for dating biological events are being increasingly questioned (Polquério & Nichols, 2007).

The reports included in this text are presented by plant group or family in Appendix 2.2. Fossils of some pteridophytes and gymnosperms extend beyond the coverage of this text into the Jurassic, Triassic, and even into the late Paleozoic (e.g., Stockey, 1977, 1978, 1982; Stockey & Taylor, 1978; Dettmann & Clifford, 1992; Mohr & Lazarus, 1994), and the tables and appendices list primarily the Late Cretaceous and Cenozoic parts of these records.

Ferns and allied groups (Stockey & Rothwell, 2006)—The origin and early diversification of the ferns occurred much earlier than the time period covered in this text. However, the record from the Cretaceous onward provides information useful for paleoenvironmental reconstructions, and it illustrates a point relevant to identifications and phylogenies. The first record for some fern genera listed in Appendix 2.2 is Cretaceous and Paleogene, while for others it is Oligocene and Miocene. Taxa cited by modern generic names according to the original authors are as follows:

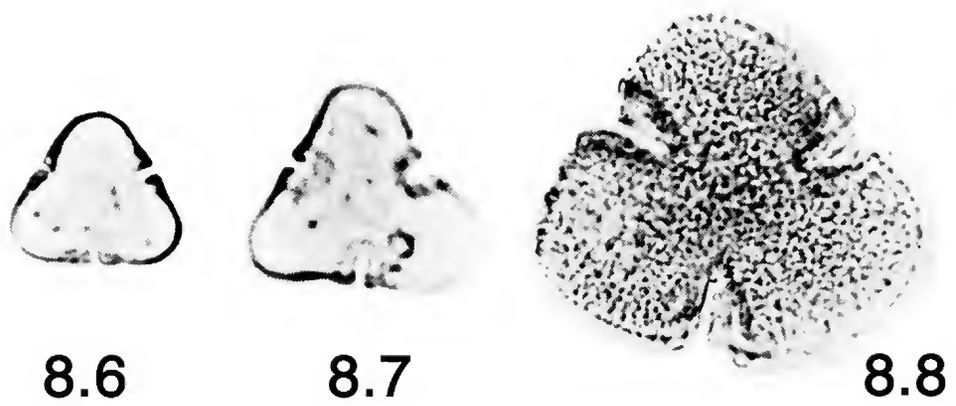
Cretaceous: *Adiantum*, *Azolla*, *Blechnum*, *Hymenophyllum*, *Schizaea*;
Eocene: *Asplenium*, *Ceratopteris*, *Dicksonia*, *Pteris*, *Woodwardia*;
Oligocene: *Acrostichum*, *Alsophila*, *Anemia*, *Antrophyum*, *Cnemidaria–Hemitelia*, *Cyathea*, *Gleichenia*, *Grammitis*, *Gymnogramma*, *Jamesonia–Eriosorus*;
Miocene: *Ctentis*, *Danaea*, *Lygodium*, *Ophioglossum*.

One criterion suggested earlier for assessing reports in the paleobotanical record is whether very old occurrences, and very young first occurrences, are consistent with proposed phylogenies. If so, both the phylogeny and the fossil record are strengthened; if not, the identifications are highlighted for additional consideration (Chapter 7, South America). Applying this guideline to the above list, genera considered basal in the developing phylogeny, such as *Azolla*, *Hymenophyllum*, and *Schizaea*, are expected in the older deposits; derived clades such as *Adiantum* and *Blechnum* are less expected; and basal genera such as *Danaea*, *Lygodium*, and *Ophioglossum* may be anticipated in deposits older than the present record indicates. Genera that are derived, and do appear later in the above list, are *Cnemidaria–Hemitelia*, *Ctentis*, and *Jamesonia*.

If an adequate global fossil record of a clade is known, it is also possible to estimate whether the first occurrence in Latin America is an evolutionary or a migrational event. Using the range charts in Germeraad et al. (1968), *Ceratopteris* (*Magnastriatites howardii*) is listed first in the late Eocene of Borneo, and not until the early Oligocene of Nigeria and South America (primarily in the Maracaibo Basin region); *Mohria* type (*Cicatricosisporites dorogensis*) occurs first in the early late Eocene of South America, and then in the middle late Eocene of Nigeria; and *Lygodium microphyllum* type (*Crassoretitriletes vanraadshooveni*) is found in the Oligo–Miocene of Nigeria, the early Miocene of Borneo, and the late Miocene of South America. As the range and identification of more genera are better established, the paleobotanical record provides increasingly precise information on the migratory history of modern lineages. Furthermore, the temptation to circumvent the frustratingly imperfect fossil record in phylogenetic analyses of the ferns has led to some imaginative if not wholly convincing relationships: "Contrary to the expectations of some, inclusion of extinct taxa in analyses of morphological characters produces striking changes in the topology of the resulting vascular plant tree when compared with the analysis of living taxa only" (Rothwell & Nixon, 2006, p. 737).

Gymnosperms—The same criteria may be applied to the

Figure 8.5. Angiosperm leaf fragment from the Aptian (121–112 Ma) Baquero Formation, Patagonia, Argentina. From Romero and Archangelsky (1986). Used with permission of *Science*, American Association for the Advancement of Science, Washington, D.C.



Figures 8.6–8.8. Late Cretaceous bombacaceous pollen from the Campanian (Figs. 8.6, 8.7) to the Maastrichtian (Fig. 8.8), Atlantic Coastal Plain, New Jersey. These are the oldest generally accepted fossils of the Bombacaceae (Muller, 1981), and the more advanced type (Fig. 8.8) appears later (Paleocene) and without transitional forms in Latin America. From Wolfe (1975), used with permission of the Missouri Botanical Garden, St. Louis.

presence of gymnosperms in the younger and older strata in Latin America:

Cretaceous: *Araucaria*, *Dacrydium*, *Podocarpus*;

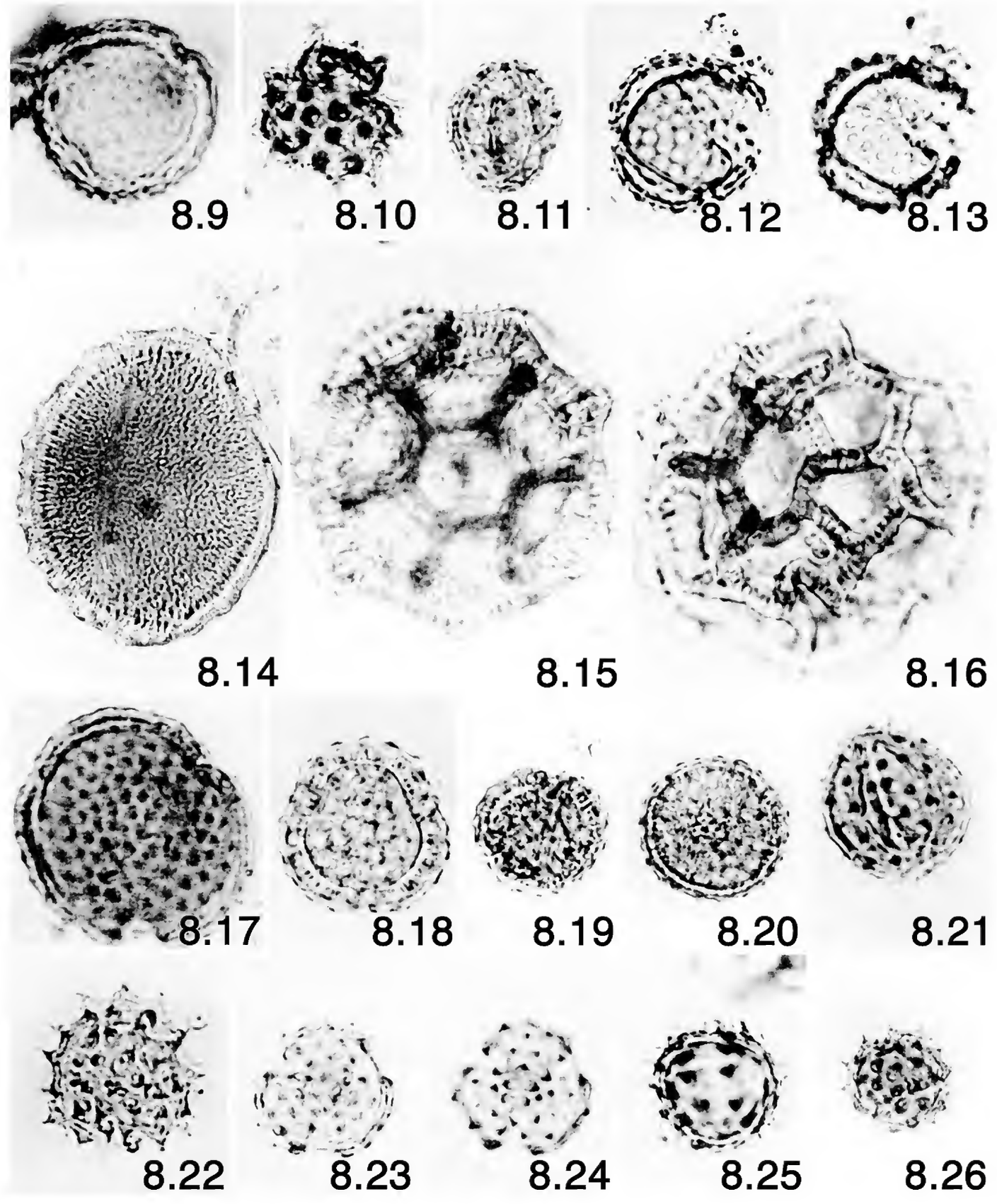
Eocene: *Fitzroya*, *Ginkgo*, *Libocedrus*, *Zamia*.

Araucaria and *Zamia* are old lineages, and *Podocarpus* appears in South America in the Eocene (van der Hammen & Hooghiemstra, 2000). *Abies*, *Picea*, and *Pinus* are more derived, their oldest records are in the temperate regions to the north (*Pinus* 128 ± 4 Ma, Eurasia; Eckert & Hall, 2006), and their appearance in South America is likely a migrational event.

Angiosperms—Among the oldest angiosperms reported for Latin America are unnamed specimens from the Baquero Formation of Santa Cruz Province, Patagonia, of Aptian age (Cretaceous, 121–112 Ma; Fig. 8.5). They are similar to leaves of the Hamamelidaceae, and in the Baquero flora they are associated with >100 species of pteridophytes and gymnosperms, typical of Middle Cretaceous assemblages (Romero & Archangelsky, 1986; Sergio Archangelsky, pers. comm., 2005). Angiosperm leaves and fruiting structures are also known from the Aptian or Albian Crato Formation of Brazil (Mohr & Friis, 2000; Mohr & Rydin, 2002; Mohr & Eklund, 2003; Mohr & Bernardes-de-Oliveira, 2004; Chapter 7, Brazil). The oldest convincing angiosperms generally are from ~130 Ma (Early Cretaceous; Friis et al., 2006), so the South American occurrences are within the time of their early radiation.

Bombacaceae: According to Wolfe (1975), the oldest records of this presently tropical to subtropical family of the New and Old World are small, faintly reticulate pollen grains with short colpi diagnostically situated in the interapical areas (Figs. 8.6, 8.7). They are from the Campanian (83.5–71.3 Ma) of the Atlantic Coastal Plain of New Jersey. Later in the Cretaceous (Maastrichtian, 71.3–65 Ma), larger and more distinctly reticulate forms of a *Cavanillesia* type appear that are typical of modern Bombacaceae (Fig. 8.8). Muller (1981) accepts these as the oldest convincing fossils of the family and notes that Bombacaceae pollen appears later in South America (Paleocene; early Paleocene in India fide Mandal, 2005), then in Africa (Paleocene–Eocene boundary), and finally in Australia and New Zealand (Eocene) without transitional forms, implying introduction of an already evolved lineage. In another prominent tropical family, the Lauraceae, "by far the oldest unquestionable…fossils have been described as *Mauldinia mirabilis* by Drinnan et al. (1990) from the Cenomanian of Maryland" (Rohwer, 1993, p. 277), "with their considerable Neotropical representation primarily derived from early Miocene radiation of the *Ocotea* complex upon reaching South America" (Chanderbali et al., 2001, p. 104; for a proposed Laurasian origin of the Melastomataceae see below).

Asteraceae (Figs. 8.9–8.26): Identification of all pre-Eocene specimens attributed to the composites are questionable, but new finds of more recent material are narrowing estimates of the time and place of origin of the family. The earliest records of Asteraceae in Latin America are mid- to high-spine pollen forms described as *Echitricolporites* (Astereae–Heliantheae–Helenieae) from sediments considered late Eocene in age from the state of Rio de Janeiro, Brazil (de Lima & Silva Amador, 1985), and Mutisieae types from the Eocene to middle Oligocene in Malleco Province, Chile (Palma-Heldt, 1983). However, there are problems with the morphology (some look malvaceous) and the documentation of these specimens (e.g., some lack descriptions and/or illustrations; see Graham, 1996). The most convincing fossils appear in the late Oligocene, but these are so diverse and widespread that it is assumed that the family likely evolved in the Eocene (Bremer, 1994; DeVore & Stuessy, 1995; Bohm & Stuessy, 2001), probably from the Calyceraceae–Goodeniaceae complex. The most frequently mentioned places of origin are Brazil excluding the Amazon Basin (Bremer, 1994; central to southern South America, Gra-



Figures 8.9–8.26. Fossil pollen of the Asteraceae from the Tertiary of northern Latin America. 8.9. Cucaracha Formation, early Miocene, Panama (27 μm), 8.10, 8.11. Artibonite Group, Miocene, Haiti (30 μm), 8.12, 8.13. Culebra Formation, early Miocene, Panama (26 μm), 8.14. Gatún Formation, late middle to late Miocene, Panama (68 × 60 μm), 8.15–8.26. Paraje Solo Formation, middle Pliocene, Veracruz, Mexico (8.15, 8.16: 63 μm, 8.17: 45 μm, 8.18: 37 μm, 8.19: 27 μm, 8.20: 30 μm, 8.21: 34 μm, 8.22: 34 μm, 8.23, 8.24: 30 μm, 8.25: 30 μm, 8.26: 27 μm). Figs. 8.9, 8.10, 8.21–8.26 are of the *Echitricolporites spinosus* type, 8.12, 8.13 *E. macneillyi* type, and 8.15, 8.16 *Fenestrites spinosus* type. The rest are described under various generic names, or as "Compositae–short spine type." From Graham (1996). Copyright The Board of Trustees of the Royal Botanic Gardens, Kew.

ham, 1996), southern South America (Bohm & Stuessy, 2001), and southern South America including adjacent Antarctica and Australia (DeVore & Stuessy, 1995). Africa is considered one of the least likely ancestral areas.

There are two recent reports relevant to the time and place of origin of the family. One is Asteraceae pollen from the late Oligocene San Julián Formation in the Playa La Mina area (Province of Santa Cruz, Patagonia; Barreda, 1997b, pers. comm., 2005). Fossil plants have been studied extensively in this region, and this is the oldest convincing record of the family in Patagonian South America. It is consistent with a site of origin that included central to northern South America in the Eocene with introduction to the south by the late Oligocene. However, Zavada and de Villiers (2000) have reported composite pollen (*Tubuliforidites antipodica*, *T. viteauensis*, Mutisieae) from the Paleocene–Eocene of western South Africa. If confirmed, it would suggest the family originated in the southern African part of Gondwana. At this time (~55 Ma) southern Africa and southern South America had been separated for ~75 Ma, and the northern parts for ~35 Ma and were half or more of their present distance apart. The time and place of origin of the Asteraceae are still not fully resolved.

Fagaceae: *Nothofagus* (Nothofagaceae) is a genus of ~35 species in southeastern Australia, New Caledonia, New Guinea, New Zealand, Tasmania, and southern South America (Veblen et al., 1996). In the most recent classification (Hill & Read, 1991), the species are distributed among four subgenera (*Brassospora*, *Fuscospora*, *Lophozonia*, *Nothofagus*), and studies of pollen morphology (Dettmann et al., 1990), molecular systematics (Manos, 1997), and geography correlate well with the subgenera. For example, subgenus *Brassospora* is tropical New Caledonian and New Guinean in distribution, and subgenus *Nothofagus* is temperate southern South American. The genus has traditionally been placed in the Fagaceae closely aligned to *Fagus*. However, there are obvious biogeographic difficulties in explaining the presence of a predominantly Northern Hemisphere family in eastern Australasia and southern South America beginning in the Cretaceous (*Quercus* appears in South

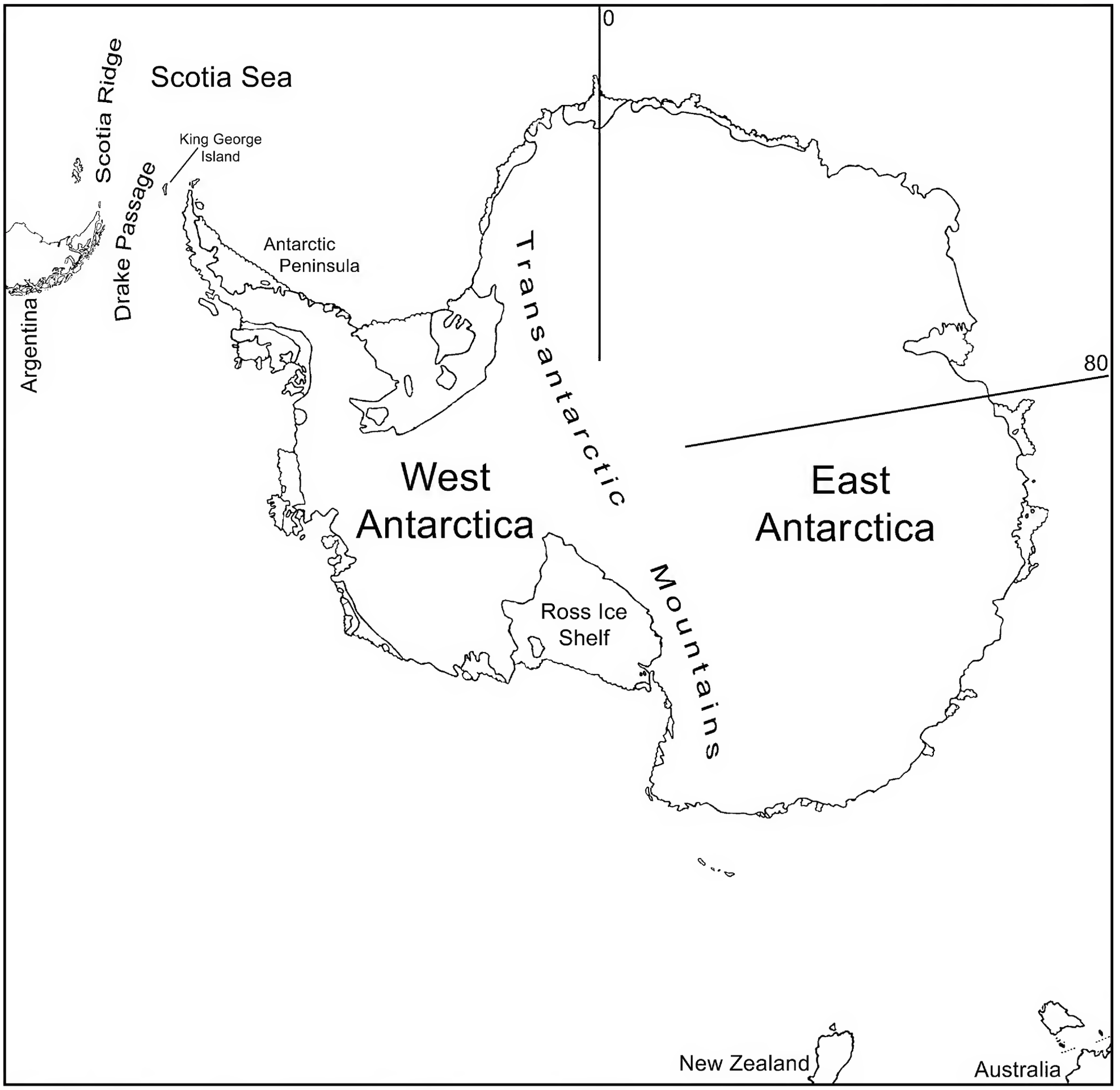


Figure 8.27. Index map of Antarctica and adjacent regions mentioned in the text.

America in the late Quaternary; *Trigonobalanus* has no fossil record in Latin America; see Chapter 3, Colombia). It has been suggested that *Nothofagus* be placed in a separate family (Nothofagaceae) or closely aligned with the Betulaceae. This would hardly simplify the historical biogeography of the group, and the familial relationships of the genus remain unresolved. The trend is to place it in the Nothofagaceae. The seeds are poorly designed for wind transport, so early vicariance (Manos, 1997; Nelson & Ladiges, 2001; McLoughlin, 2001; Swenson & Hill, 2001; Swenson et al., 2001) together with rare long-distance dispersal (MacPhail et al., 1994) are the likely means of distribution.

Fossil leaves and wood of *Nothofagus* are known but are not highly diagnostic, and reproductive structures are rare. Pollen, described as *Nothofagus* and *Nothofagidites*, is distinctive, eurypalynous, wind dispersed, and abundant in the fossil record (e.g., Romero, 1973). Dettmann et al. (1990) have clarified much of the taxonomic confusion of the fossils resulting from improper typification and nomenclature and the loss or misplacement of specimens. Their system of naming the pollen categories is complicated, but among the 36 fossil pollen species (plus two others described by Zamaloa, 1992, and Zamaloa & Barreda, 1992), the oldest are designated "ancestral type a" and are represented by *Nothofagidites senectus*, which is

most similar to pollen of the modern *Nothofagus fusca*. *Nothofagidites senectus* is listed in the early Campanian (~83.5 Ma) of western Antarctica and southern Australia, and the genus *Nothofagus* is described as having evolved in southern South America–Antarctica–Australasia. *Nothofagidites* is not listed for the Campanian of South America, but it is included by Harris (1974) in DSDP core assemblages from the South Atlantic Ocean with the Campanian dinocyst index species *Nelsoniella aceras*. The earliest on-land occurrences of *Nothofagidites* cited for South America are *N. rocaensis* from the middle Maastrichtian Jagüel Formation of Río Negro Province (~70 Ma) and *N. dorotensis* from the late Maastrichtian–early Paleocene Cerro Dorotea Formation of Santa Cruz Province (~65 Ma). These are ~13.5 Ma or more later than the age cited for Australasia and Antarctica. Many of the older records in the early literature need confirmation (Michael MacPhail, pers. comm., 2005).

After its initial appearance, early diversification of *Nothofagus* did take place in West Antarctica–southern Australia–southern South America (Fig. 8.27), and that region has been designated as a Late Cretaceous and Paleogene biotic province called Weddellia (Fig. 8.28). It is a convenient reconstruction for envisioning migration of the southern biota through the high southern latitudes. Note there are no connections to Africa or India, and neither modern nor fossil *Nothofagus* are known from these continents. The general sequence of vegetation on Antarctica, based on fossil woods, is summarized by Cantrill and Poole (2005) as follows: Aptian–Albian (125–99.6 Ma; podocarpaceous, araucarian, minor taxodiaceous–cupressaceous conifers), Cenomanian to Santonian (99.6–83.5 Ma; extinct angiosperms), Campanian–Maastrichtian (83.5–65.5 Ma; modernization, including appearance of *Nothofagus*). Forests of *Nothofagus* developed across southern South America beginning in the middle Eocene (49–41.3 Ma; Melendi et al., 2003; Barreda & Palazzesi, 2005) in the absence of an effective Andean mountain barrier (Hinojosa & Villagrán, 2005).

The Neogene occurrence of *Nothofagus* is useful for reconstructing environments in West Antarctica. After isolation of the continent ~30 Ma, temperatures began to cool significantly toward the Oligocene–Miocene boundary (~24 Ma), and there was a marked reduction in plant diversity. On King George Island, Cretaceous and Paleocene species of *Nothofagus* with large, broad leaves were replaced by smaller-leaved species after the Oligo–Miocene. The last occurrence of *Nothofagus* reported for Antarctica is pollen, leaves, and krummholz stems from the Pliocene Sirius Group in the Transantarctic Mountains. Minimum winter temperatures above –22° C, and above 0° C for other months of the year, are required for *Nothofagus*, and this would mean conditions warmer there than the present by ~13° C (Hill, 2001; Hill & Dettmann, 1996). Temperatures continued to cool through the late Cenozoic, with further simplification of the vegetation, so that now there are only two naturally occurring vascular plants on the continent—*Colobanthus quitensis* (Caryophyllaceae) and *Deschampsia antarctica* (Poaceae).

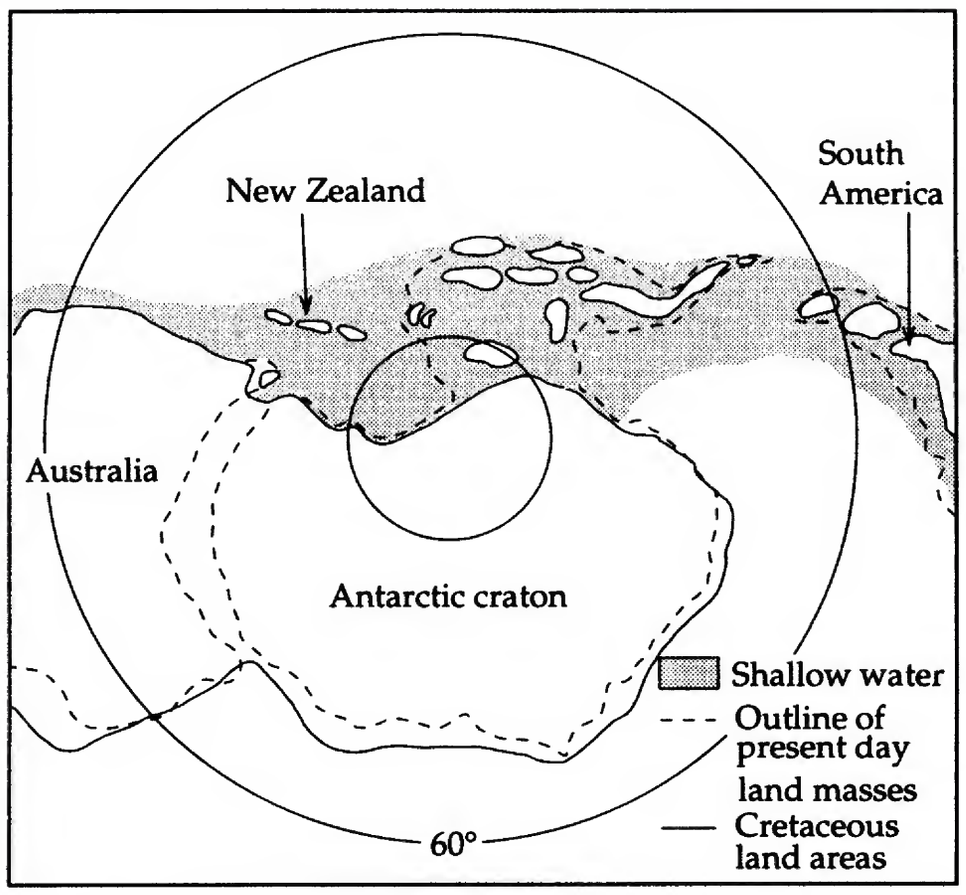
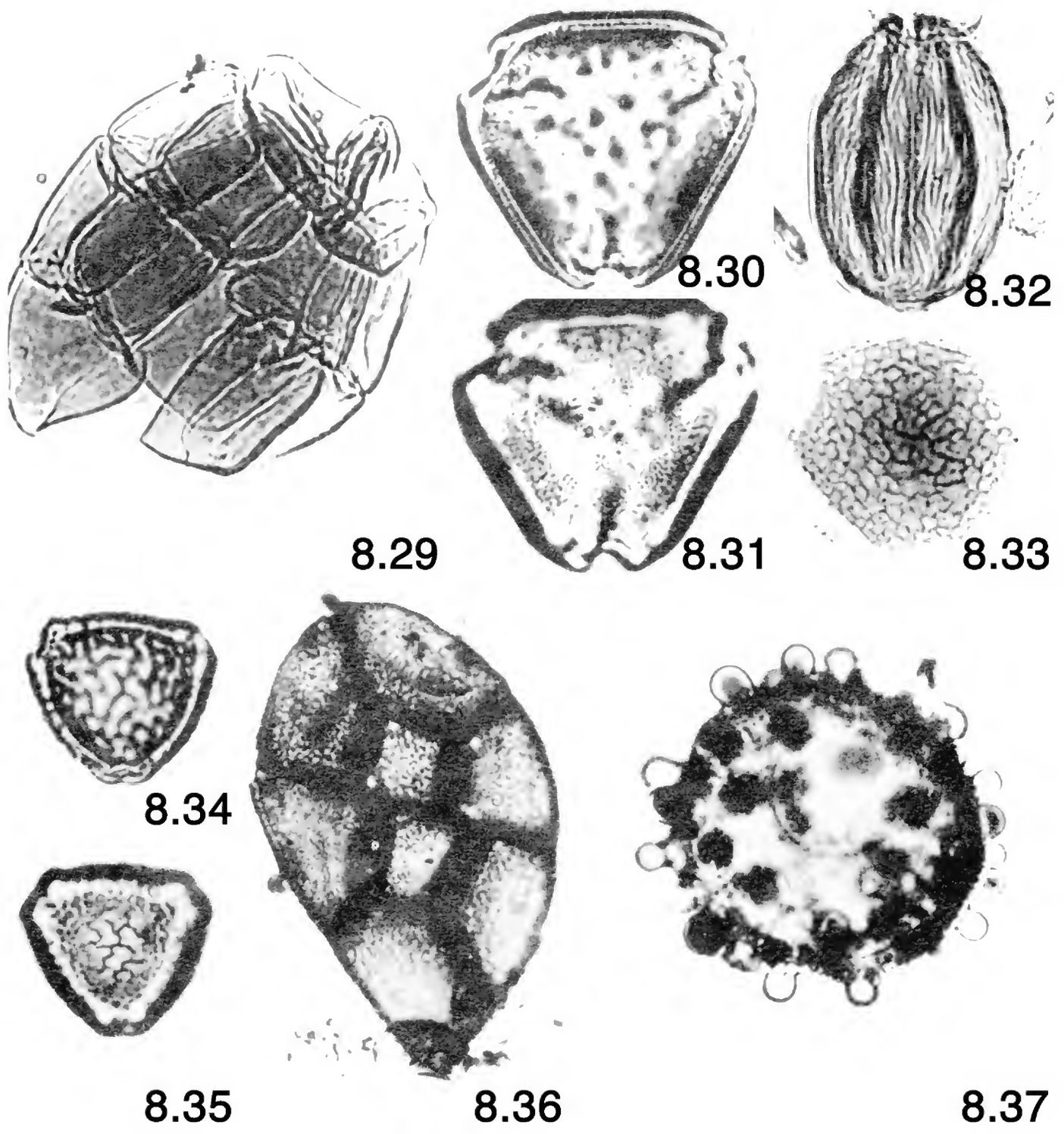


Figure 8.28. Reconstruction of Weddellia during the Cretaceous and Paleogene. Stippled area represents continuous coastal environment surrounded by shallow seas. From Hill and Dettmann (1996). Used with permission of Yale University Press, New Haven, CT.

Fabaceae (Figs. 8.29–8.37): The greatest diversity among extant genera of the legumes is in Africa–Madagascar and in South America. The Latin American fossil record is important because the oldest remains attributed to the family are coeval between Siberia, Canada, and Colombia (Muller, 1981). The latter is pollen described as *Sindorapollis villaltai* (aff. Caesalpinioideae) from the Late Cretaceous (Maastrichtian) of the Magdalena Valley (Sole de Porta, 1972). The affinity of the pollen and several Cretaceous fossil woods attributed to the family is uncertain, however, because the observable morphological features are not uniquely synapomorphic for the family; i.e., specialized features restricted to the Fabaceae (Herendeen et al., 1992). By the Paleocene, and especially by the Eocene, the family was diverse and widespread, and all three subfamilies are represented (e.g., in the early Eocene of the southeastern United States). Other reports of the Caesalpinioideae are *Margocolporites vanwijhei* (*Caesalpinia* type) and *Striatopollis catatumbus* (*Crudia* type) from the Paleocene–Eocene of Colombia (Jaramillo & Dilcher, 2001; cf. *Crudia* from the middle–late Eocene of Panama, Graham, 1985, 1992b; Appendix 2.2). Latin American occurrences of the Mimosoideae, also appearing in the Eocene, are reported by Caccavari (1996), Caccavari and Anzotegui (1987), Caccavari and Barreda (2000), and Barreda and Caccavari (1992; Appendix 2.2). The early record of the Papilionoideae is uncertain because many genera have generalized tricolporate reticulate pollen, in contrast to the distinctive polyads of most Mimosoideae and the elaborate entomophilous types of some Caesalpinioideae (e.g., *Bauhinia*; I: p. 119; Graham & Barker, 1981). The early megafossils of papilinoid legumes in South America are leaflets referred to *Cassia* (common), *Dalbergia*, *Desmodium*, *Inga*, *Schizolobium*, and cf. *Senna*, mostly by Berry, and all need verification. The fact that the



Figures 8.29–8.37. Fossil Fabaceae pollen from Cenozoic deposits of northern Latin America. 8.29. *Acacia* (54 μm), Culebra Formation, early Miocene, Panama. 8.30, 8.31. *Canavalia* (55 μm), Gatún Lake, Quaternary, Panama. 8.32. *Crudia* type (46 × 30 μm), late middle to late Miocene, Gatún Formation, Panama. 8.33. *Erythrina* (35 μm), Gatún Formation, Panama. 8.34, 8.35. *Erythrina* (35 μm), Gatún Lake, Panama. 8.36. *Calliandra* (215 × 135 μm), Gatún Lake, Panama. 8.37. *Bauhinia* (110 μm), Gatún Lake, Panama. Figs. 8.30, 8.31, 8.33–8.37 from Bartlett and Barghoorn (1973).

oldest fossils attributed to the legumes are uncertain, and that they occurred at about the same time in Siberia, Canada, and Colombia, means the time and place of origin of the family are uncertain.

Melastomataceae: Presently there are ~3000 species of the family in the Neotropics, 1000 in tropical Asia, 240 in Africa, and 225 in Madagascar. The historical biogeography of the Melastomataceae is currently under study, and there are two views about its place of origin and subsequent radiation. Renner et al. (2001; Renner & Meyer, 2001) believe on the basis of molecular evidence, and a study of the fossil record, that the Melastomataceae initially diversified in the Paleocene–Eocene north of the Tethys Sea (viz., in Laurasia). The earliest megafossils are leaves from the early Eocene (53 Ma) of North Dakota and from the middle Eocene (50–48 Ma) of Washington State. During the Oligocene and Mio–Pliocene (35–5 Ma), the family spread through North America and Eurasia. A well-preserved leaf (*Melastomaceophyllum danielis*; Fig. 8.38) was described from Colombia (Departamento de Antioquia, Cordillera Occidental) in beds cited as Eocene by Huertas-G. (1977), but now regarded as Oligocene (Renner et al., 2001; Susanne Renner, pers. comm., 2005). The leaves show the characteristic campylodromous venation of the Melastomataceae in which tertiary veins run at right angles to the primary (midvein) and secondary veins. The family is proposed to have spread from the Neotropics to Africa 14–12 Ma, then to Madagascar, India, and Indochina. It had achieved its approximate present distribution by the Neogene as a result of long-distance dispersal rather than fragmentation of Gondwana (Renner et al., 2001).

Morley and Dick (2003) believe the fossil record is not sufficient to accurately calibrate the molecular data, and that the rates of synonymous nucleotide substitutions derived by Renner et al. (2001) are up to three times faster than most published rates. According to Morley and Dick (2003), the rates fall within the range of published values, assuming a Gondwanan origin and migration from Africa to Southeast Asia.

As noted, in Latin America the oldest megafossil Melastomataceae is the leaf from the Oligocene of Colombia. Pollen of the family is small, psilate, and tricolporate with three alternating pseudocolpi lacking pores (heterocolpate). This combination is characteristic of the Melastomataceae, but it also occurs in the Combretaceae and in the Lythraceae (Graham et al., 1985, 1987, 1990). Melastomataceae-type pollen has been described from the Paleocene of Colombia (*Heterocolpites palaeocenica*; van der Hammen & de Mutis, 1966) and the Eocene of Colombia (*H. paluster*; González-Guzmán, 1967; Fig. 8.39).

Figure 8.38 (left). Leaf showing the characteristic venation of the Melastomataceae from the early middle Eocene (50–48 Ma) Republic flora of Washington State, U.S.A.). From Renner et al. (2001).

Figure 8.39 (right). Pollen of *Heterocolpites paluster* from the Eocene of the Tibú area, Colombia. The features of size (22 × 17 μm), shape (prolate to prolate–spheroidal [oblong]), sculpture (psilate [smooth]), and heterocolpate condition (three colpi with pores, three without pores) are similar to those of the Melastomataceae. From González-Guzmán (1967).

If these suggested biological affinities are correct, it would place the family in northern South America (Gondwana) at about the same time to slightly earlier than its earliest occurrences in North America (Laurasia). However, recall there is some paleobotanical evidence that the present-day predominantly tropical families Bombacaceae, Lauraceae, and others may also have had a Laurasian origin.

Onagraceae: The record of the Onagraceae in Latin America is important because, like the Fabaceae, the South American fossils are among the oldest attributed to the family. There is pollen described as *Jussitriporites* by Pares Regali et al. (1974b) from the Late Cretaceous of Brazil that is about the same age as *Trivestibulopollenites* (cf. Onagraceae, Campanian–Maastrichtian) and *Vacupollis* (probably Onagraceae, Maastrichtian) of California (see review by Martin, 2003, table 5).

Rubiaceae: There are several facets of the fossil record of the Rubiaceae that are typical for a large number of angiosperm families. One is that the published overall record bears little similarity to the one based solely on verifiable fossils from accurately dated horizons. Altogether, there are 73 taxa in deposits as old as the Late Cretaceous described in 115 publications (Graham, 2009). Closer scrutiny reveals, however, that among the phylogenetically important of these fossils from the Cretaceous and Paleocene, several were studied in the late 1800s, the biological affinities of others cited in the stratigraphic literature were casual, informal references, none have been verified, and others cannot be located in repositories and are apparently lost. Another fact that becomes apparent from the long and tedious efforts required to compile the fossil record of a family, as noted previously, is the unorganized state of the information. For the Rubiaceae, based on newly gathered and evaluated reports, the oldest verified records are megafossils of *Emmenopterys* from the middle Eocene of Oregon and Washington (Manchester, 1994; Wehr & Manchester, 1996) and the dimorphic pollen of *Faramea* from the late Eocene of Panama (Graham, 1985). This illustrates an increasingly recognized common pattern whereby convincing records of a family go back to about early to middle Eocene, but the diversity and extensive range of distribution indicates an earlier origin and radiation in the Late Cretaceous and Paleocene (Anderson et al., 2005). Beyond that, the characters become more general and plesiomorphic and mostly suggest complexes from which the modern families were derived. Exceptions are modern families regarded as toward the base of the angiosperms and recognizable in more ancient deposits (e.g., Cunoniaceae [*Platydiscus peltatus*] from the Late Cretaceous of Sweden; Magnoliales [*Endressinia brasiliana*] from the Early Cretaceous Crato Formation of Brazil; Friis et al., 2006) and those regarded as derived and that appear later (e.g., Asteraceae from the Eocene/Oligocene).

ORIGIN OF THE NEOTROPICAL RAIN FOREST

Estimating the nebulous beginnings of an ecosystem is based on the gradual appearance in the geological record of characteristics that in combination are accepted as defining that ecosystem. In the case of the Neotropical rain forest, these are (1) a community dominated by angiosperms, (2) occupying mostly lowland (<700 m) and relatively flat terranes with high water tables, and (3) growing under climates that are generally warm and moist throughout the year (Chapter 3, Brazil). After the rain forest became established, it was possible to recognize it more readily in the fossil record by features typical of the modern version (e.g., presence of Fabaceae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Arecaceae as prominent families [Burnham & Johnson, 2004], drip-tips, leaves with entire margins, wood with no or poorly developed growth rings, overall large size, lianas, epiphytes, and diversity). The angiosperms had become prominent over much of the landscape by the Late Cretaceous (~90 Ma). Afterwards, climates in the LPTM–EECL provided suitable MAT and MAP at a time when flat, low-lying landscapes were extensive. Sea levels were up to ~300 m above present levels, and water tables were correspondingly high. This combination of the available plant constituents, physiography, habitats, and climate was attained in the Paleocene (early Paleocene fide Morley, 2000; later in the Paleocene–Eocene fide Ziegler et al., 2003), and this is the time the syndrome of morphological features common to the rain forest become increasingly apparent in fossil assemblages. It is also the time when a significant increase in biodiversity is evident in Neotropical fossil floras (Jaramillo et al., 2006). Thus, the Paleo-

cene–Eocene is regarded as the interval when the rain forest in a modern sense became defined (Burnham & Johnson, 2004; Morley, 2000; ~55–58 Ma). Recent paleobotanical studies have clarified its subsequent history, particularly with regard to earlier assumed stability over geologic time, and have contributed a useful historical component to models attempting to explain the origin of its signature levels of biodiversity.

CLIMATE, VEGETATION, AND THE STABILITY OF TROPICAL ECOSYSTEMS

> "The earth's climate has never been stable. Climate has varied on all timescales… ." (Markgraf, 2001, p. xix)

The revelation that equatorial SSTs and the climates of adjacent coastal areas in the Paleogene and Cretaceous were about as warm or warmer than at present might suggest that tropical terrestrial environments and biotas have existed essentially unchanged through long periods of geologic time. This impression is reinforced by the subtle but nonetheless real impact that the lowland tropical rain forest often makes on first-time visitors. The sensory experience of a silent, dense, incredibly diverse, moist to wet, dark, unfamiliar vegetation with huge trees festooned with ferns, lichens, bryophytes, and lianas, with snakes the size of anacondas, grasses the size of bamboos, and ferns as large as small trees has caused many observers to wax eloquently about an ancient and primeval forest. It is mostly evergreen without a noticeable leaf fall, and flowering and vegetative regeneration generally occur unobtrusively throughout the year. So it seems unchanging from season to season, and this easily segues into an impression that it is equally unchanging from epoch to epoch:

> "It is likely that in some at least of the regions where Rain Forest is now the climatic climax, similar vegetation has extended uninterruptedly since a very remote geological period." (Richards, 1964, p. 14)

According to Ashton: "The complexity of the rain forest can be explained in terms of (i) The seasonal and geological stability of the climate—(ii) Their great age." In reference to Dobzhansky (1950), Ashton noted "the great stability of tropical ecosystems in geological time" (1969, p. xx), and commented that the forests of the Malayan uplands "appear to have remained above sea level and probably under a uniform climate since the Cretaceous" (1969, p. xx). Ashton further referenced the "ancient stable environment of the tropics." (Ashton, 1969, p. 155)

> "Still less is known of the geological history of the Amazon and Congo forests [than the Indo–Malaysian forest], except that they must have existed in modern dress since Eocene times…. Thus the Cretaceous forests were modern systematically…. The geological record shows that in all major aspects the evolution of flowering plants has been at a standstill since the Cretaceous." (Corner, 1958, p. 36)

The paleontological basis for these impressions, prevalent through the 1960s, is elusive. As a graduate student at the University of Michigan during this period, I heard lectures by Rogers McVaugh stating that the lowland tropical rain forest was one of the most diverse assemblages of organisms ever to occupy the Earth, and others by Warren H. Wagner Jr. indicating that instability, environmental change, and stress at the limits of a species' range were conducive to the generation of novel genotypes and phenotypes. I recall it seemed incongruous that the most species-rich of all vegetation types, and its environments, should be stable and unchanging. An effort to find paleobotanical evidence either way revealed how little information was available. Later, during postdoctoral studies on Neotropical paleocommunities, the paradox came to mind, and the fossil flora from the middle Pliocene Paraje Solo Formation of Veracruz, Mexico, provided an opportunity to consider it in greater detail (Graham, 1976a, b).

As noted in Chapter 4, the lignites of the Paraje Solo Formation were deposited along the coast, and in the modern setting, this zone is fringed seaward by mangrove forests and immediately inland by tropical rain forest. A variety of communities are represented in the microfossil flora including *Quercus* and *Liquidambar* from the deciduous forest association within the lower to upper montane broad-leaved forest, *Quercus* and *Pinus* from the upland pine-oak association and the coniferous forest, and even *Abies* and *Picea* from the highland coniferous forest. Lacking was representation of the ~8 co-dominant trees of the tall evergreen selva (Fig. 3.53; Appendix 1.1) and most of the associated genera found only or primarily in rain forest vegetation. By the 1970s, evidence was accumulating from systematic-biogeographic studies (Haffer, 1969, 1974; Vanzolini, 1973; Vanzolini & Williams, 1970; review by Vuilleumier, 1971) and from high-altitude sites in the Colombian Andes (van der Hammen, 1961; van der Hammen & Gonzalez, 1960a, b) that Quaternary climate changes must have affected the lowland tropical rain forest to some extent. The Paraje Solo study provided the initial paleobotanical support for this view. Since the 1970s, a broad array of information has accumulated, particularly for the Quaternary, to show that rather than being stable and unchanging, the rain forest and other tropical biological formations and associations are delicately balanced assemblages that have changed significantly in range and composition throughout geologic time. The dynamic aspect of the Latin American environment is evident in the geologic summaries (Chapter 2), and it is reflected in virtually all vegetational histories presented in the database (Chapters 4–7). In the Late Cretaceous, there was the asteroid impact and subsequent recovery period, early rise of the Sierra Madre Occidental and Sierra Madre Oriental, separation of South America from Africa, sea levels higher by up to ~300 m and falling, and continental interiors were flooded and beginning to

drain. In the Paleogene, temperatures rose to their highest in all of Phanerozoic time then began to decline, the Greater Antilles emerged in the Eocene, and South America separated from Antarctica in the Oligocene. In the Neogene, there was the rise of the Transvolcanic Belt in Mexico, closure of the Isthmus of Panama, elevation of the Andes Mountains to about half their present height, a reversal in the flow of the Amazonian rivers from into the Pacific Ocean to eastward into the Atlantic Ocean, and a rise in temperature to the middle Pliocene climate optimum followed by a decline leading to the Quaternary glaciations. During the latter interval, a myriad of environmental changes occurred, including 18–20 glacial advances and retreats, the Younger Dryas, Little Ice Age, Heinrich and D–O events, and human impact, all documented in tropical latitudes. Overprinted on these changes were Milankovitch variations, fluctuating CO_2 concentrations, solar variations, changing thermohaline concentrations and ocean currents, epidemics, extinctions, and evolution. Thus, from the modern perspective, it is difficult to perceive of any extensive period from the Late Cretaceous to the present when environments and vegetation in the tropics were stable and unchanging. One benefit of the new view, beyond clarifying an important aspect of Neotropical vegetation history, is that it removes the rationalization that the rain forest can be exploited with impunity because it has recovered from previous perturbations and existed in modern dress for millions of years. The modern literature reflects the new paradigm:

> "Since 1952 ecological ideas, including the author's, have changed in many respects. The old notion of the stability of rainforests over long periods of time has been replaced by a dynamic concept of rain forests as kaleidoscopic mosaics continually reacting to climatic changes and human pressures." (P. W. Richards, 1996, p. xvii, with contributions by R. P. D. Walsh, I. C. Baillie, and P. Greig-Smith)

REFUGIA

> "…nothing in nature is so obligingly straightforward." (Fortey, 2004, p. 111)

> "[He] doth protest too much, methinks." (Shakespeare, *Hamlet*, Act 3, Scene II)

A discussion of refugia has been deferred to last because it is an interesting and unresolved problem in tropical biology. It illustrates two principal themes of this text—the need for a systems approach to complex, multifaceted topics, and the need for conclusions evaluated within a broad context of information derived from independent lines of inquiry. History has shown that initial reactions to new ideas, ranging from evolution to plate tectonics, often include enthusiastic acceptance as well as demands for their complete abandonment ("the academic-scientific community immune system"; Linden, 2006, p. 90), frequently followed by modifications that over time produce an acceptable version.

The concept

To insure an accurate basis for discussing refugia, it is worthwhile to begin with Jürgen Haffer's (1969, p. 131) original statement of the concept as applied to the Amazon Basin:

> "…during several dry climatic periods of the Pleistocene and post-Pleistocene, the Amazonian forest was divided into a number of smaller forests which were isolated from each other by tracks of open, nonforest vegetation. The remaining forests served as 'refuge areas' for numerous populations of forest animals, which deviated from one another during periods of geographic isolation. The isolated forests were again united during humid climatic periods when the intervening open country became once more forest-covered, permitting the refuge-area populations to extend their ranges. This rupturing and rejoining of the various forests in Amazonia probably was repeated several times during the Quaternary and led to a rapid differentiation of the Amazonian forest fauna in geologically very recent times."

That aspect of the theory attempting to explain high levels of diversity in the extant tropical biota is not readily addressed through paleobotany. It is not possible to determine with certainty, for example, if species richness is greater now than in the Neogene, or if peaks of enrichment followed the glacial–interglacial cycles (the engine of diversity). An alternative view is that environmental stability results in low extinction rates and allows for the accumulation of species (Amazonia as a museum; see Colinvaux, 1997; Colinvaux et al., 1999). The refugium concept is most compatible with the engine model, while the museum viewpoint implies that versions of the rain forest existed across the lowlands throughout the glacial and interglacial stages of the Quaternary.

In fact, there is some evidence for an actual decrease, or at least fluctuations, in overall plant diversity at times during the Neogene and Quaternary. Hoorn (1994) records ~280 pollen types in Miocene river valley sediments in northwestern Amazonia, while Urrego-Giraldo (1994, 1997) lists half that number (~140) in comparable deposits of Holocene age in the Colombian Amazon. Wijninga (1996) also sees a decline in diversity during the Miocene, Pliocene, and Quaternary in Colombia, and Flenley (2005) notes "that palynological richness has probably declined during the Quaternary." The repeated isolation and contact of forest elements in the Quaternary may have promoted speciation, and it may account for the high levels of diversity in some groups of organisms, but environmental instability also causes extinctions. A modifying nuance of the above trends, if correct, is that although the kinds of organisms have changed, neither engines nor museums produced a net increase in diversity in recent geologic times. Another

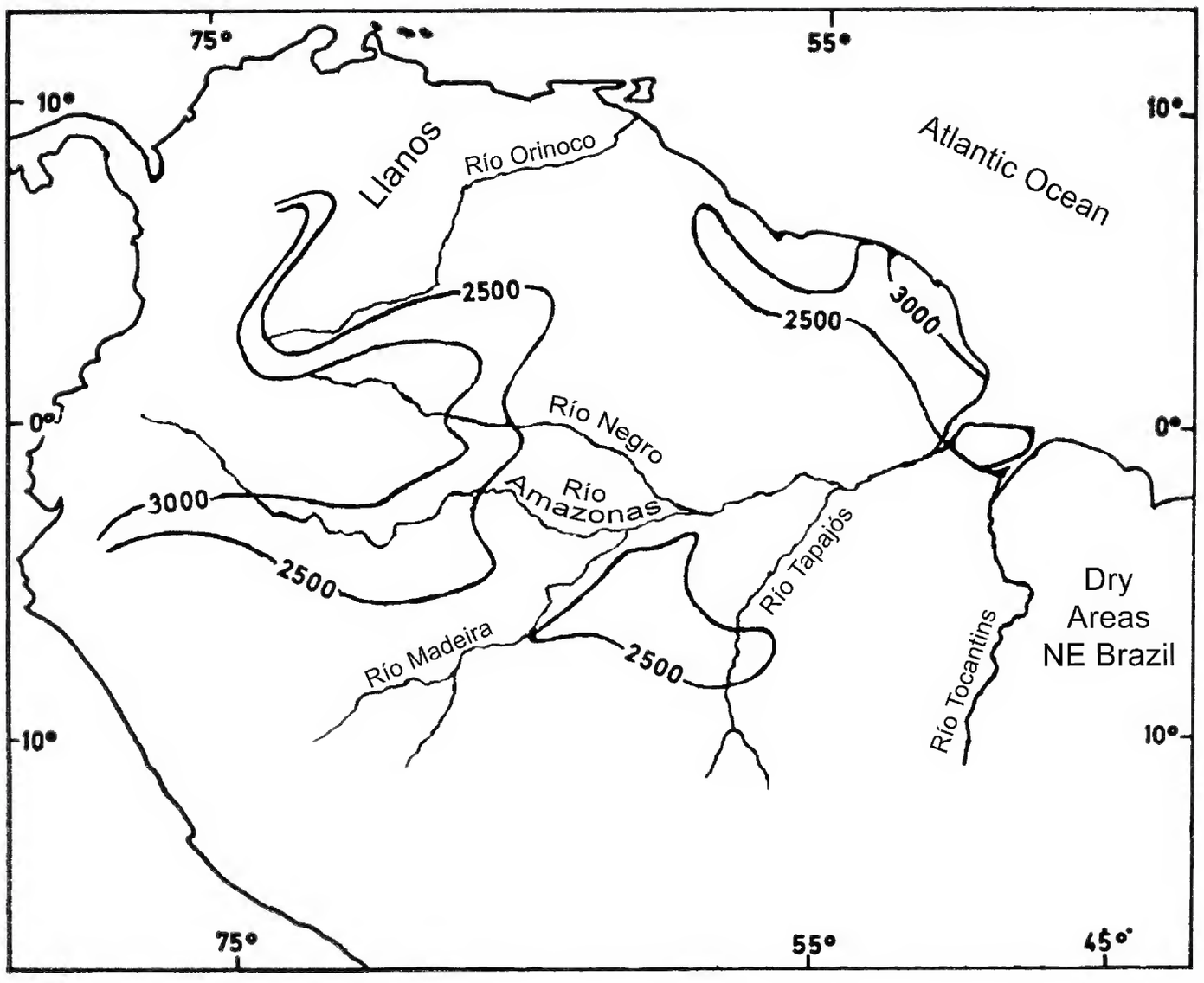


Figure 8.40. Areas of high MAP in the Amazon Basin. Based on Haffer (1969). Adapted from K. Hueck, Die Wälder Südamerikas (Fischer, Stuttgart, 1966); J. Haffer, Amer. Mus. Novit. No. 2294; Auk 84, 343 (1967); A. Aubréville, Étude écologique des principales formations végétales du Brésil. (Centre Technique Forestier Tropical, Nogent-sur-Marne, France, 1961); and W. M. Deneven, Ibero Americana 48, 7 (1966). Reprinted with permission of AAAS.

observation related to diversification in the tropics is that the tempo of molecular evolution may be greater than at higher latitudes (Wright et al., 2006, p. 7718): "…tropical plant species had more than twice the rate of molecular evolution as closely related temperate congeners." If so, increased warmth toward the tropics, overall global warming as at present, and increases at intervals in the geologic past may have had several effects pertinent to tropical biogeography and diversification. These include intensifying the strength, frequency, and duration of El Niños and hurricanes, and enhancing speciation rates because "mutagenesis occurs more frequently as productivity and metabolic rates increase toward the equator" (Wright et al., 2006, p. 7718). Thus, long-term climate trends join spatial fragmentation of ranges through arches, drainage systems, and possibly refugia in the paleo-component of any unified explanation for the diversity of tropical biotas. The implications for molecular clocks is also obvious if the rate of mutagenesis within and between lineages can vary over time with place and temperature. Equally obvious, and consistent with a thesis of this text, is the inadequacy of simplistic explanations, often involving the word "versus," for complex phenomema that would seem intuitively likely to involve a system of factors. Thus, it is not surprising that the view is emerging that the tropics are both a cradle and a museum with greater importance depending on the lineage under consideration (Jablonski et al., 2006; Marshall, 2006).

Those aspects of the refugium concept that can be most directly addressed through paleobotany are (1) did cold intervals affect the Neotropical lowlands, (2) did dry periods accompany these cold intervals, and (3) were dry periods sufficient to reduce the moist forest to isolated locales and promote expansion of drier forest, savanna, and/or grassland into the intervening areas.

Two criteria were used by Haffer (1969, 1970, 1974, 1982) to identify potential refugia—present-day areas of high precipitation (MAP 2500–3000 mm or more), and areas of high concentration of bird superspecies. Three areas of high precipitation were recognized (Fig. 8.40): (1) upper Amazonia, west toward the base of the Andes Mountains where rainfall becomes even greater, and northeast to the Chocó–Golfo de Urabá region (Haffer, 1970); (2) between the Rio Madeira and Rio Tapajós region; and (3) southwestward from the southern Guianas, and eastward toward the mouth of the Rio Amazonas. The minimum MAP in regions presently supporting tropical rain forest is ~2000 mm. In the intervening regions where MAP is ~1500 mm or less, there is drier forest, savanna, or grassland as, for example, in the zone connecting Los Llanos and the dry areas of northeastern Brazil (Chapters 1, 3). Thus, a reduction in MAP of ~25% (from 2000 to 1500 mm), or a more pronounced dry season, would favor drier vegetation over the present moist forest. Local areas of dry vegetation also occur scattered in the lowlands on hilltops and on edaphically dry sandstone outcrops.

Areas identified by Haffer as having high concentrations of bird superspecies were upper Amazonia and toward the base of the Andes Mountains, south of the Rio Amazonas from the lower Rio Tapajós east to the Atlantic coast, and from the Guianas west to the Rio Negro and south–southeastward to the Rio Amazonas. Others were later recognized in Central and South America (Haffer, 1974; Whitmore & Prance, 1987).

These early proposed refugia are shown in Fig. 8.41. The perceived correspondence between wet areas and high levels of avian diversity was the basis for the theory of refugia.

Haffer's (1969) presentation was not one of advocacy, and it certainly was not adversarial: "The interpretation should be considered merely a working model based on a number of inferences. It may, however, serve for testing the distribution pattern of various groups of organisms. Much more concrete information on the climatic and vegetational history of Amazonia, as well as on the population structure and species relationships of Amazonian birds and other animals, is needed if one is to reconstruct the actual course of species formation in particular areas or in certain families." The terms "aridity" and especially "extreme aridity" were not used in Haffner's original presentation, and they are too limiting to impose on changes in vegetation accommodated within the refugium concept. As Simpson (1997) notes, their use renders objections to the concept open to the criticism of setting up a straw man against which opposing views can be contrasted. Haffer did not suggest that arid vegetation covered all the landscape between refugia; rather, he allowed for "tracks of open, nonforest vegetation."

Somewhat prophetically, Haffer (1969) noted that "even when palynological field data from Amazonia become available, it will remain difficult to map the distribution of forest and nonforest vegetation at any given time under the constantly changing climatic conditions of the Pleistocene." Palynology is mentioned specifically because it is an important technique for tracing the Quaternary history of vegetation and environments in the tropics (Prologue). In evaluating the palynological results, several factors are worth noting:

(1) The time span within the Quaternary covered by the spore and pollen data for the Amazon Basin is mostly the Holocene and just back into the last glacial stage: "Only seven pollen records located in the Amazonian rain forest area including the Amazon fan date back to the Last Glacial Maximum: Katira (9°S, 63°W), Carajás (6°S, 50°W), Hill of Six Lakes (0°16'N, 64°4'W), Maicurú (0°30'S, 54°W), Laguna Bella Vista (13°37'S, 61°33'W), Laguna Chaplin (14°28'S, 61°04'W), ODP Site 932 (5°13'N, 47°2'W)" (Anhuf et al., 2006). It is not known whether the precipitation, temperature, and biotic fluctuations of the last Late Glacial and postglacial cycle (~70 Kyr) reflect the full extent of changes during all 18–20 glacial cycles of the past 2.6 Ma; it does seem clear that Pleistocene dryness at the last glacial–interglacial transition (~12 Kyr) does reflect these changes, but to an uncertain extent (I: pp. 276–279). The assumption is that the last interval is typical, but paleobotanical data from the coldest parts of the 18–20 previous cycles would be valuable, and that information is not available.

(2) The limitations of palynology (I: pp. 117–121), as applied to Late Glacial and postglacial sediments, become ever greater when applied to progressively older cycles; that is, interpretations become less certain the farther the paleocommunities are removed from modern analogs. Several of these limitations are relevant to detecting the presence and extent of tropical lowland plant formations. For example, differential preservation precludes the presence of the important rain forest family Lauraceae in the microfossil record (*Ocotea*, ~350 species; *Nectandra*, ~120 species; *Persea*, ~100 species in tropical to warm-temperate America). Differential production reduces representation of entomophilous humid forest trees. Montane species present the simultaneous difficulties of overproduction by some (wind-pollinated species), underproduction by others (animal-pollinated species), varied distances from the site that change through time, and redeposition–differential transport by rivers and sheet-flow into the basins. Some of these problems are overcome through modern pollen rain studies that can provide baseline data for comparison, but the results are limited by human disturbance of the extant analog vegetation, and they apply mostly to the latest version of the communities that resulted from the most recent phase of climate reshuffling. This means that both the former presence and the extent of montane vegetation in the lowlands is difficult to reconstruct from pollen assemblages. Refugia located in the deeper river valleys (e.g., the upper Magdalena Valley) would not be easily detectable from lake and bog material outside the valleys. Pollen and other paleobotanical remains preserved in river deposits are susceptible to transport from other sites, and material in deltaic and offshore sediments are particularly difficult to interpret (see later discussion).

For a long time (e.g., since Geisler, 1945), attempts have been made to distinguish grass species based on pollen, but without success. It is also impossible to differentiate between pollen of savanna and marsh grasses. In theory, this means that large amounts of grass pollen cannot be used as evidence for dry forest–savanna–grassland vegetation because the pollen could represent marsh grasses or species invading temporarily dry bog surfaces or lake margins (Colinvaux et al., 1999; Bush, 2002). Usually, however, drying episodes are accompanied by changes in the natural vegetation (e.g., fewer fern spores and palm pollen), geology (lower sea levels and erosion of terraces), and sediments (more dust and charcoal except where caused by human disturbance). Additionally, there are other elements indicating savanna and grassy savanna vegetation, such as *Byrsonima*, *Curatella*, and *Stryphnodendron*, along with *Caryocar* and *Cuphea* (widespread and found in other habitats). The fact that grass pollen in some assemblages may come from marsh species does not mean that grass pollen can never be used as suggestive of savanna or grassland in any assemblage; that is too broad a generalization. In the absence of evidence to the contrary, large or increasing amounts of grass pollen are most parsimoniously explained as a trend toward reduced or more seasonal precipitation favoring drier vegetation. The refugium model cannot be proved or disproved in an absolute sense, and the quest is for a balanced assessment of probabilities. The process is weakened by a factor-by-factor analysis concluding that, because each factor has some limitation, none of the proposed supporting or detracting evidence is valid.

Pollen and spore analysis provides what may be called indications of past vegetation and environments. It is not a qualita-

Figure 8.41. Presumed Quaternary refugia in Central and South America according to Haffer (1974). 1 = Caribbean Central America, Guatemala–Honduras, 2 = Caribbean Costa Rica, 3 = Pacific Central America, 4 = Pacific Colombia, 5 = Caribbean Colombia, 6 = Catatumbo, 7 = Northern Venezuela, 8 = Napo, 9 = Eastern Peru, 10 = Imerí, 11 = Tepui, 12 = Guyana, 13 = Madeira–Tapajós, 14 = Pará, 15 = Goiás, 16 = Cerra do Mar. Black area = mountains above 2000 m. Used with permission of the Nuttall Ornithological Club, Cambridge, Massachusetts.

tively or quantitatively exact tool, and relying on it too heavily to support or refute such complex issues as refugia over the 2 Ma of Quaternary time exceeds the sensitivity of the method. Gosling et al. (2005, p. 284) found that although most of the major pollen producers are represented in the modern pollen rain at Noel Kempff Mercado National Park (Bolivia), "75% of stems and 67% of the total basal area of the plot ≥10 cm d.b.h. belong to species which are unidentified in the pollen rain." The vagaries of the technique impart some choice in interpretation, and the choices become greater in progressively older material. Where one methodology does not provide the definitive answer, ancillary evidence is essential. However, regardless of whether this evidence suggests coolness, dryness, warmth, moisture, or stability, there is usually enough leeway in spore and pollen diagrams to see some support for a favored position. A realistic expectation is that the indications from palynology will be paralleled by sufficient independent evidence to suggest a most-probable model-for-the-moment. The accuracy of radiometric dates is essential when reconstructing regional vegetation, and periodically these dates need to be revised, verified, or retracted.

(3) The use of data and methods transgress from objectivity to advocacy if inconsistencies, deficiencies, supporting, or opposing evidence are trivialized to produce a model near-perfect in detail. The issue of refugia is too complex not to have points against it and points in its favor.

(4) If the evaluation of a concept focuses narrowly on the original or early versions, then its rejection is probably preordained. In the case of refugia, it is useful to know if the moist lowland forest was more restricted at glacial maxima than at

Figure 8.42. Index map of principal Quaternary palynofloras in the Amazon Basin of Brazil. (See also Fig. 8.44; van der Hammen & Hooghiemstra, 2000, fig. 1.) Used with permission of Elsevier Science Publishers, Amsterdam.

present and if it persisted along the banks and floodplains of major rivers (gallery environments), in the deeper river valleys, at the confluency of major rivers, at places along the base of the Andes Mountains, or anywhere in the Amazonian region. It is also useful to know if at these times dry vegetation was more extensive. It is less useful to know or debate if details in the original depiction of refugia presented 40 years ago were exact. Broad concepts rarely emerge in final form without need for modification (Simpson, 1997). The refugium concept has not been afforded that opportunity, and the task is to see if it can be modified into a useful way of envisioning rain forest dynamics, or if it should be abandoned.

Support

With the basic tenets of the refugium theory presented (Haffer, 1969, 1970, 1974, 1982), the distributions of other plant and animal groups were examined to see if the concept and locations for refugia were generally applicable and if there was a plausible mechanism. Early results were presented at a symposium on biological diversification in the tropics (Prance, 1982) and in a later summary (Whitmore & Prance, 1987). The groups analyzed included plants (e.g., Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, Lecythidaceae; Prance, 1973), insects (*Heliconius* butterflies; Brown, 2005; Brown et al., 1974), frogs, fishes, and birds (toucans, jacamars). The consensus was that sufficient correlation existed between localities of high precipitation and high biodiversity to support the concept. The causal mechanism was assumed to be alternating cold-dry and warm-humid climates. Stone lines were interpreted as evidence for dryness (Ab'Saber, 1982), and the few spore and pollen studies available suggested that cool temperatures and dryness disrupted the lowland Amazonian rain forest (van der

Hammen, 1972, 1982; see also Absy, 1982; Salgado-Labouriau, 1982).

The palynological evidence was that around the borders of the rain forest, savanna vegetation, including *Byrsonima* and *Curatella*, periodically expanded (e.g., in the Guianas) at times corresponding to lower sea level. Pollen diagrams from Los Llanos Orientales and the Rupununi savanna indicated that open grass savanna replaced savanna woodland (with *Byrsonima*). Within the Amazon Basin, palynological data from Katira (Rondônia; 18,500 ^{14}C years B.P.; van der Hammen, 1972, 1982; Absy & van der Hammen, 1976; Fig. 8.42), outside the proposed Madeira–Tapajós refugium, suggested alternating sequences of forest and grassy savanna where arboreal pollen nearly disappears (the latter correlated with an increase in valley- and colluvial-type eroded sediments), while in central Amazonia Holocene deposits in a gallery forest setting showed persistence of rain forest with little or no indication of savanna vegetation. Other early support came from studies of the extant biota:

> "All botanical evidence [e.g., high endemism] is consistent with the persistence of one or more forest refuges in the Chocó during the dry periods associated with ice age glacial advances" (Gentry, 1982, p. 112);
>
> From other botanical evidence (areas of high endemism, persistence of xerophytic plants as relicts of drier climatic periods), "it is concluded that 26 areas of lowland forest endemism were probable forest refuges at the time of reduction of forest cover" (Prance, 1982, p. 150); and
>
> At six tropical lowland sites, including Ecuador, Peru, and Bolivia, "Historical factors in the form of Pleistocene forest refuge theory…were highly accurate in predicting the rank order of bird species numbers on these six plots." (Pearson, 1982, p. 441)

Since this early period of mostly enthusiastic endorsement of the refugium concept, additional palynological studies have been completed (see Chapter 7, Brazil and below). This literature is reviewed by Hooghiemstra and van der Hammen (1998), who include a bibliography of more than 500 papers on the Neogene and Quaternary history of the Amazon Basin (see also van der Hammen & Hooghiemstra, 2000). For the Chocó, palynological studies on pre-Holocene sediments are not available, but cores dating back 6000 years contain spores and pollen of rain forest taxa throughout this time; e.g., *Acalypha*, *Alchornea*, *Cecropia*, *Euterpe–Geonoma*, *Mimosa*, *Piper*, *Protium*, *Sloanea*, *Socratea*, *Wettinia*, Fabaceae, Melastomataceae–Combretaceae, and Moraceae–Urticaceae (Behling & Hooghiemstra, 1998).

In Amazonia, temperatures at the Last Glacial Maximum (18 Kyr) were lower than at present by an estimated 4.5° ± 1° C (van der Hammen & Hooghiemstra, 2000) to 4° ± 2° C

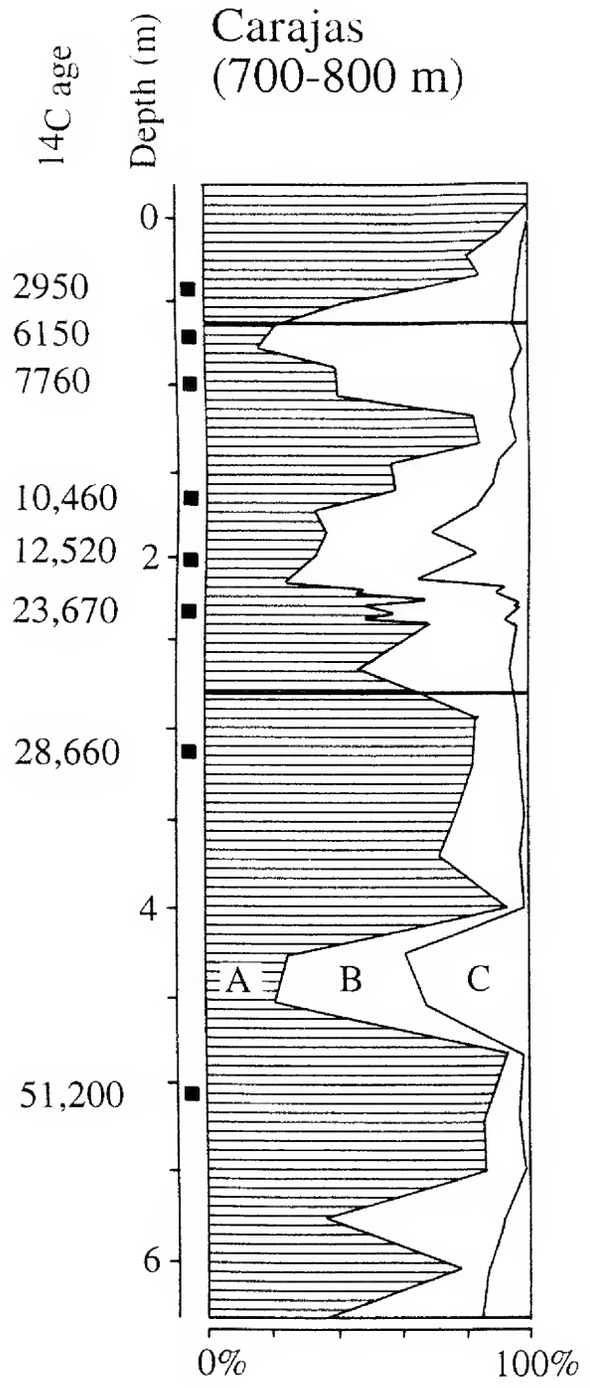


Figure 8.43. Pollen records from Carajás (Brazilian lowland forest). A = trees, B = Poaceae, C = Asteraceae + *Borreria* + *Cuphea*. Note fluctuations between AP (arboreal) and NAP (non-arboreal) pollen. Reprinted from Hooghiemstra and van der Hammen (1998), with permission of Elsevier Science Publishers, Amsterdam.

(Hooghiemstra & van der Hammen, 1998). These estimates would presumably apply generally to the previous 18–20 glacial maxima of the Quaternary, and the Milankovitch periodicities predict that the cool and dry intervals lasted considerably longer than the warm and humid ones (~90 Kyr and 10 Kyr, respectively, within each 100-Kyr eccentricity cycle; I: pp. 35–40). At Salitre in east-central Brazil (Fig. 8.42), spore and pollen records indicate fluctuations in precipitation and periods when the lake surface was dry (Ledru, 1993). Also in east-central Brazil, two >25-Kyr records at Vereda de Aguas Emendadas and Cromínia (from *Mauritia* swamps within predominantly cerrado vegetation; Ferraz-Vicentini & Salgado-Labouriau, 1996; Fig. 8.42) indicate early cerrado vegetation with grass pollen reaching ~80% at glacial intervals, a later, even drier interval between 19 and 7 Kyr B.P., and intervening more moist conditions (Salgado-Labouriau et al., 1998). The presumption is that if a *Mauritia* swamp in east-central Brazil dried out, or was significantly reduced, rain forest was not likely present uniformly across Amazonia at that time.

A summary diagram from the top of a low table mountain (700 m) at Carajás in eastern Amazonia is shown in Fig. 8.43. The present vegetation at the top is edaphic dry forest, shrub, and open savanna, surrounded by rain forest. The MAP is 1500–2000 mm, right at the dividing line between rain forest and dry forest–savanna–grassland precipitation. Sediments dated back to ~60,000 years show high lake levels and forest vegetation dominated at 55, 35, and 6 Kyr, and low lake levels with savanna vegetation at 65, 40, and 23–13 Kyr, approximately reflecting the precessional cycle of ~20,000 years. Evidence for this cycle, also present in the Funza core (~50, 28, 6 Kyr), is important because it suggests a forcing mechanism for possible shifts in the ITCZ that would influence, and complicate, Quaternary precipitation patterns in the equatorial latitudes (later section). It further suggests a tie between temperature and precipitation in the lowlands, making it difficult to accept periods of lower temperatures without acknowledging often greater dryness. Van der Hammen and Hooghiemstra (2000) note that "the remarks in Colinvaux et al. (1996; Colinvaux, 1997) that grasses and herb components are high throughout, and that the arboreal elements are associated with the open vegetation of the site, are incorrect... ." At and after ~6000 years B.P., increases in charcoal may indicate dry periods, but humans have been in the area since ~8000 years B.P. Later work at the Rondônia site (van der Hammen & Absy, 1994) showed rain forest with *Mauritia* swamps at ~50,000 years B.P., grass savanna at the LGM (~18,000 years B.P.), and rain forest since that time.

The Noel Kempff Mercado National Park is located in the lowlands of northeastern Bolivia near the boundary with the Brazilian states of Rondônia and Mato Grosso. Two lakes (Laguna Bella Vista and Laguna Chaplin) at 200–250 m elevation are in the lowland Amazon rain forest and near the Huanchaca Plateau (600–900 m) covered by savanna. Cores with sediments dated back to 50 Kyr show savanna and seasonally dry semideciduous forest for most of the time, and especially at the LGM. A mixture of evergreen and semideciduous vegetation expanded between 6 and 3 Kyr, and rain forest became established ~2 ^{14}C Kyr B.P. (Burbridge et al., 2004). A reconstruction of possible vegetation patterns in Amazonia at the LGM is shown in Fig. 8.44.

Attempts have been made to read lowland vegetation history from palynomorphs retrieved from deltaic and offshore sediments. This is difficult for a number of reasons, including redeposition and intermingling of spores and pollen from Neogene, glacial, and interglacial deposits, and the filtering of pollen from savanna grasses and shrubs growing distant from the rivers by forest and gallery forest vegetation. This is shown by the Orinoco River delta study discussed in Chapter 3 (Venezuela) where mixing of sediments and the dominance of local vegetation is evident. The profiles typically have the expected degree of sameness throughout, and they, as well as pollen from offshore cores, are not the strongest basis for inferring the history of onland vegetation.

In summary, there are palynological indications of alternating humid (forest) and dry (savanna) intervals to the north (Guianas, Los Llanos Orientales, Rupununi savanna, Lake Valencia), to the west (Colombian Andes), to the east in east-central Brazil (Vereda de Aguas Emendadas, Cromínia), and to the south and southwest in Amazonian Brazil (Carajás, Rondônia; and to some extent at Pata; see below) and in the Bolivian lowlands. Humid conditions persisted in the Chocó, at Araracuara and mostly at Pata, constituting refugia there; these conditions also presumably persisted in the present-day wettest areas at the confluency of major rivers, in deep valleys, and in floodplain and gallery forest environments, and possibly in the super-wet area at the bend of the Andes Mountains.

Objections

Early on, it was observed that the refugium theory was rapidly being used to explain disjunctions and speciation in a wide range of organisms, and that acceptance was coming too easily:

> "Among people who are favorably disposed to the theory as a means of understanding South American biological diversity, there is an attitude of uncritical, weak corroboration. Data are being fit into the model quite enthusiastically. This has given the unsatisfying result…that virtually all of tropical South America has now been claimed…[as a refuge for] at least one taxon. Of course, Haffer has been more cautious and exclusive about which sorts of distributions should be taken as evidence for the theory. It would be useful to ask what sort of patterns are predicted not to occur by the refuge theory" (Strong, 1982, p. 158);

> "Evolutionary relationships among representative *Leptodactylus* [frog] species based on comparative studies of albumin sequence differentiation…reveal that speciation events are Tertiary, not Pleistocene events. The refuge theory accounts for very few distributional events and no speciation events in the *Leptodactylus* complex" (Heyer & Maxson, 1982, p. 375); and more recently,

> "In the ancient Amazon region, carbon isotope data for the toxodonts indicate a C_3-based tropical rainforest habitat with no evidence for grasslands as would be predicted from the Neotropical forest refugia hypothesis." (MacFadden, 2005, p. 113)

Another concern was the suggestion that some higher elevation sites in Panama were refugia because, even in drier times, rainfall still would increase upslope to moderate elevations (Whitmore & Prance, 1987; Chapter 6, Panama). These are not the most convincing locales for rain forest in drier times, and Bush and Colinvaux (1990) are unequivocal in their assessment: "The wet highlands of Panama were never refugia for tropical rain forest taxa at any time during the Quaternary… ."

Mera is located in the Amazon lowlands of Ecuador. The

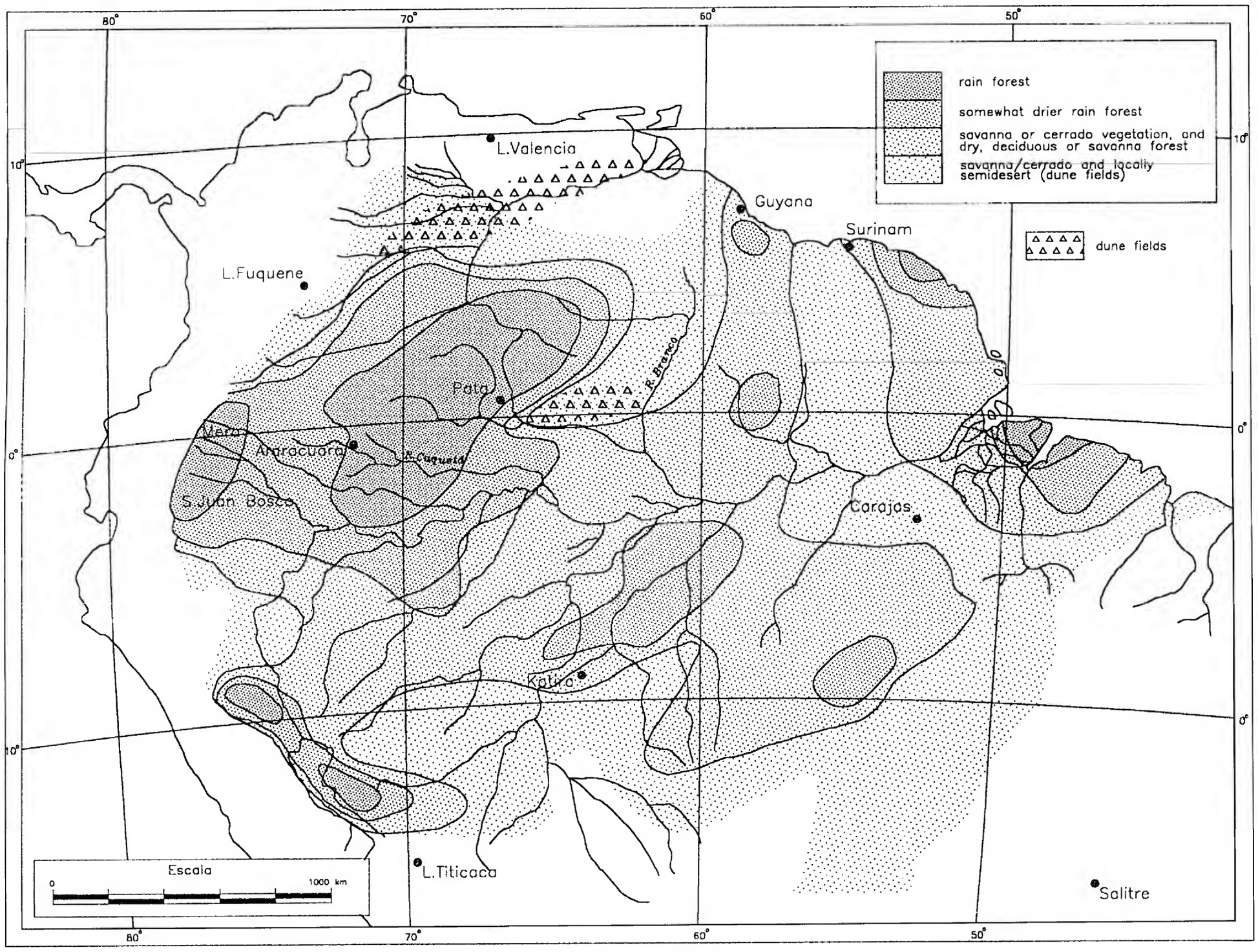


Figure 8.44. An interpretation of vegetation patterns in the Amazon Basin and adjacent areas at the LGM suggested by palynological and other data, based on the rainfall map of Figueroa and Nobre (1990), and assuming a reduction in rainfall of ~40%. According to the recent version of the refugium theory, during the interglacials the range of the rain forest–somewhat drier rain forest would expand into the (potential) near-continuous cover as at present, the savanna and associated vegetation would contract, and the process would be repeated to varying degrees during each of the 18–20 glacial maxima of the past 2.6 Ma. Reprinted from van der Hammen and Hooghiemstra (2000), with permission of Elsevier Science Publishers, Amsterdam.

elevation is 1000 m, MAT is 20.8° C, MAP is 4800 mm, and the site is near the transition between lower montane and lowland rain forest (Liu & Colinvaux, 1985; Colinvaux & Liu, 1987). The localities contain wood of *Podocarpus*, dated at 33,520 ± 1010 years B.P., and pollen of *Acalypha*, *Alnus*, *Cecropia*, *Ficus*, *Hedyosmum*, *Iriartea* and other palms, *Piper*, *Trema*, and others. The organic sediments are associated with fluvial sands and gravels with rounded stones, but it was considered unlikely that the fossils included redeposited specimens. The conclusions were that during the last glaciation MAT was ~4.5° C lower than at present, lower montane vegetation (*Podocarpus*, *Alnus*, *Hedyosmum*) shifted downward by ~700 m, cooler temperature rather than aridity (dryness) was the principal forcing mechanism for vegetation changes, and that closed tropical forest persisted in the lowlands from glacial times through the Holocene. Van der Hammen and Hooghiemstra (2000) disagree with these conclusions and believe the depositional setting and evidence from elsewhere (see below) do suggest water transport of at least some montane pollen and wood. Maize cultivation was established in the Ecuadorian lowlands and influenced the vegetation after 6000 years B.P. (Bush et al., 1989).

Heine (1994, 2000) questions the dates given for the Mera sediments, believes they "give clear evidence that the ^{14}C ages are not true ages but contaminated ages," and suggests they are older than the last glacial period. If so, supporting evidence for a downward shift in montane elements weakens because the deposits could extend back into the previous interglacial. For the region in general, he concludes from the collective evidence that LGM climates were drier than at present (see also Thomas, 2000, pp. 24–25). With reference to Amazonia generally, Maslin and Burns (2000) state that "the oxygen isotopic composition of planktonic foraminifera recovered from a marine sediment core in a region of Ama-

zon discharge shows that the Amazon Basin was extremely dry during the Younger Dryas with the discharge reduced by at least 40% compared to that of today."

Further evidence for significant dry periods comes from the Oberá Formation, a tropical loess deposit of upper Pleistocene age (probably isotope stage 4) in the Argentina–Brazil borderland. Similar deposits occur in the Manaus–Parintins region of central Amazonia (Iriondo & Kröhling, 1997; Iriondo, 1999). In the Oberá Formation, continuous stone lines recognized along the outcrop, along with sedimentary evidence for dry climates in central Amazonia, and mobilization of dune fields in the Rio Negro Basin (significant aeolian dynamics in some periods) "argues against current opinions that drastic ecological changes did not affect the Amazon during the last global glaciation" (Filho et al., 2002, p. 205).

Lake Pata in northwestern Brazil is located in present-day lowland tropical rain forest (Figs. 8.42, 8.45; the spore and pollen diagrams of Lake Pata and several other sites in Amazonia are available in Colinvaux et al., 1999). Rain forest is interpreted as present throughout the last 40 Kyr ("unequivocally forested"), based on specimens identified as *Apeiba*, *Byrsonima*, *Caryocar*, *Clusia*, *Cordia*, *Didymopanax*, *Eschweilera*, *Guarea*, *Humiria*, *Iriartea*, *Mabea*, *Macrolobium*, *Matayba*, *Mauritia*, *Pera*, *Protium*, *Psychotria*, *Sapium*, *Tapirira*, *Trichilia*, *Virola*; Appendices 1.20, 1.21, and 1.25). It was considered drier between ~30 and 14 Kyr because lake levels were lower and the sediments were oxidized. Temperatures were cooler by an estimated 5°–6° C based on the presence of pollen from typically montane trees and shrubs interpreted as relicts of cooler times. A later and longer record (170 Kyr) suggests "mesic forest throughout the last ice age" and a cooling of 4°–5° C (Bush et al., 2004).

The range in interpretations possible from spore and pollen diagrams has been noted earlier. In the case of Lake Pata, van der Hammen and Hooghiemstra (2000) believe that pollen of *Podocarpus*, *Alnus*, *Hedyosmum*, and *Ilex* is commonly blown or washed in from montane sites, and note that it is frequently mixed with pollen of lowland vegetation in Tertiary and Quaternary assemblages. They conclude, therefore, that the extent of temperature depressions implied by these elements is uncertain. Gentry (1986a, b) observed that montane plants occur today in the lowlands in areas where there is unusually high rainfall or moisture; e.g., *Podocarpus lambertii* and *P. sellowii* in gallery forests at 750 m elevation in central Brazil (De Oliveira, 1992), to nearly sea level at other sites (Gentry, 1993). Mostly, they do not grow at these elevations, however, and, just as the most parsimonious explanation for increasing grasses is drying, the presence of pollen from montane elements likely indicates cooler times. It is the quantitative implication of their presence that is unsettled.

The evidence from Pata regarding refugia is also interpreted differently by different authors. Colinvaux et al. (1996) take the data to mean that the western Amazon forest was not fragmented into refugia. Hooghiemstra and van der Hammen (1998) believe the regional forest was fragmented, that the Pata site is within a refugium area, possibly with a few more deciduous species as suggested by van der Hammen and Absy (1994), and that continuous moist forest is the expected result. The presence of rain forest is also inferred from spore and pollen diagrams from a site near Araracuara in Amazonas, Colombia, along the Caquetá River (van der Hammen, 2001).

At another locality (San Juan Bosco, Ecuador; 3°3'S, 78°27' W, 900 m elevation), Bush et al. (1990) interpret pollen of montane forest types to mean a temperature lower than at present by ~7.5° C, and that "these data of forest community change from sites lying within the postulated glacial rain forest Napo refugium, provide the strongest paleoecological refutation of the refugial hypothesis yet obtained." Van der Hammen and Hooghiemstra (2000) believe that the proposed 7.5° C lowering of temperature is too great and suggest ~2° C. As noted, they believe that "the suggested mixture of tropical and montane elements is not a special glacial time phenomenon.... It is a general characteristic of the transitionary zone between the subandean forest (lower montane forest) and the lower tropical belt; in this case, the phenomenon is apparently enhanced by pollen and wood most probably fluvially transported." The range in temperature lowering given by opponents to the refugium concept is from >4° to 7.5° C, and by proponents from 2° to 4.5° ± 1° C, and 4° ± 2° C. These estimates are important because if neither cooling at the maximum levels nor the often associated decrease in precipitation was sufficient to replace moist forest with drier vegetation at Pata, then the case for rain forest across Amazonia throughout the Quaternary is strengthened. Recent independent evidence is for a lowering of 5.5°–6° C at the LGM (Webb et al., 1997). The values for the previous glacial maxima are unknown.

In addition to the need for at least modification of the concept and relocation of some presumed refugia, it is clear that the cause(s) originally suggested for Quaternary rain forest dynamics were too simplistic. A view of vegetation formations expanding and contracting across Amazonia in concert with interglacials that were consistently warm and moist, and glacials that were cool and dry, belies the complexities driving the regional climate, such as the instability of the ITCZ and Milankovitch precession cycles superimposed on eccentricity cycles. Among factors that allow more than one opinion to emerge from a single method applied within the same basin are (1) the broad range of interpretations possible from spore and pollen diagrams, (2) the lack of sufficient megafossil evidence to narrow the range, and (3) the complexity resulting from the several components of climate, coming from different directions, and operating simultaneously across an area as extensive as Amazonia. It has been suggested, for example, that the precession cycle causes shifts in the north-south boundaries of the ITCZ. The area along the southern boundary would alternately be within and beyond the zone of high rainfall induced by the meandering ITCZ, while the central region would remain within the zone of higher rainfall (Hooghiemstra & van der Hammen, 1998).

Another variable is that trends in temperature and rainfall were different at the beginning (Early Glacial), middle (pleni-

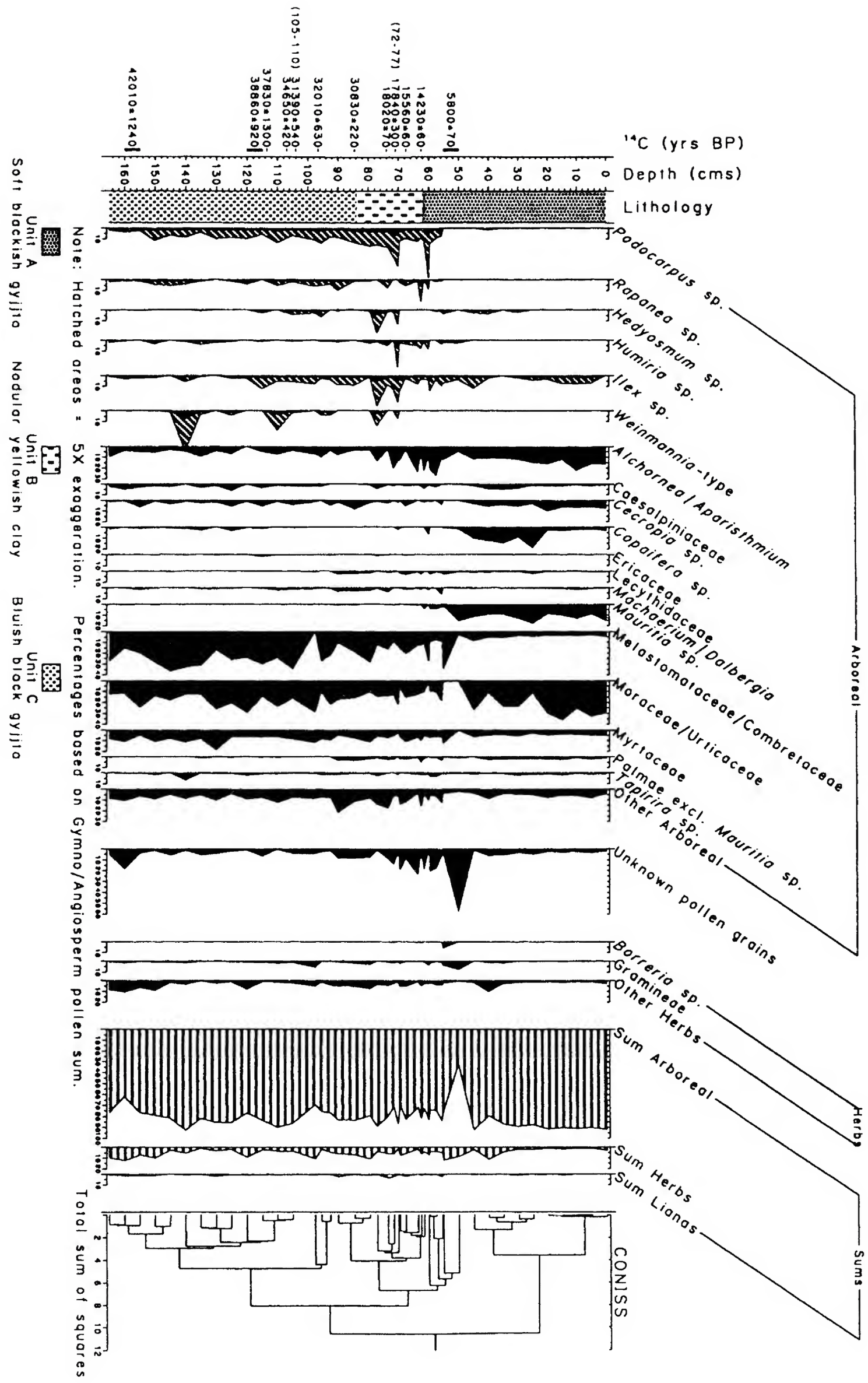


Figure 8.45. Pollen diagram from Pata, northwestern Brazil. Note little or no fluctuation in tree pollen throughout the section as shown in the Sum Arboreal column, and compare with Fig. 8.43. From Colinvaux et al. (1999). Reproduced by permission of Taylor & Francis Books, Oxford, U.K.

glacial or full-glacial), and end (Late Glacial) of the last cycle and presumably in all 18–20 cycles. Van der Hammen and Hooghiemstra (2000) propose a cool and wet middle pleniglacial (60–28 Kyr B.P.) with greater accumulation of fluvial sediments, and a cold and dry upper pleniglacial (28–14 Kyr B.P.) with increased erosion of these sediments. In the upper pleniglacial, MAP was reduced by an estimated 45% ± 10%, and lake levels were lower. This was a favorable time for expansion of dry forest, savanna, and/or grassland, compared to the middle pleniglacial and postglacial times. Thus, in the tropical latitudes, the cold/dry-warm/moist intervals resulting from the Milankovitch variations were influenced by the meandering of the ITCZ and by trends within the glacial cycles.

Independent evidence for cooling and drying in the Amazon Basin

During the 1970s and early 1980s, it was generally believed that temperature fluctuations at the Last Glacial Maximum waned toward the equator and were only 0° C to a maximum of 2° C cooler than at present (Chapter 7, South America). Subsequently, a wealth of material and a variety of techniques have established that terrestrial paleotemperatures in the Neotropical lowlands were significantly lower than at present (~5° C at the latitude of the Greater Antilles, Guilderson et al., 1994; 5.5°–6° C generally, Webb et al., 1997; 5° C in tropical Brazil, Stute et al., 1995, Aeschbach-Hertig et al., 2000). In addition to cool temperatures, relative atmospheric CO_2 concentrations varied from high (interglacials) to low (glacial), influencing vegetation through an undetermined effect on photosynthesis. Sea levels were lower at glacial maxima by ~120 m (I: pp. 92–98), constituting a third perturbation by lowering water tables with another undetermined, but presumably drying effect on soil moisture and vegetation in the lowlands. These factors collectively altered the altitudinal zonation of upland vegetation and the composition of all plant formations after each reshuffling (e.g., I: pp. 107–108). It is also agreed that the lowlands were drier, particularly at the glacial maxima (e.g., Muhs & Zárate, 2001). The disagreement is whether the combined effects of coolness, dryness, lower water tables, and lower CO_2 concentration at glacial maxima caused expansion of drier vegetation and restriction of moist forest into areas that would qualify as refugia. The principal focus now is on the degree and the effect of dryness.

The geological evidence for dryness has been reviewed and found to be wanting by Colinvaux et al. (2000, 2001, p. 609): "All geological data from Amazonian landforms imply continuous humid weathering throughout Late Tertiary and Quaternary times, with all claims for arid land processes shown to be in error," and the summary by Clapperton (1993) supporting dryness in the Amazon Basin is dismissed as based on a few undated geomorphological observations (see also Colinvaux, 2005). Acceptance of refugia is characterized as the process of shoring up a hypothesis in terminal decline, as indicated in the titles, "The failure of the aridity and refuge hypotheses" and, more pointedly, "A paradigm to be discarded: Geological and Paleoecological data falsify the HAFFER & PRANCE refuge hypothesis of Amazonian speciation" [caps by the original authors]. The terms "all," "never," and "unequivocal" are satisfyingly simple to understand, but they were "never" universally accepted and more recently are becoming less so, as applied to paleoclimates of the Amazon Basin and the refugium concept.

Studies in addition to those previously cited are lending further support for dry times in the lowlands (e.g., Lichte & Behling, 1999): "…the modern landscape presents forms [stone lines] influenced by the dry and cold climatic conditions." Mayle and Beerling (2004) studied carbon storage over the past 21 Kyr (LGM and Holocene) in relation to paleohydrological and paleoecological data. They conclude that savanna expanded near the margins of the Amazon Basin, and that southern Amazonia "may have been covered by deciduous/semi-deciduous dry forest rather than evergreen rain forest" (p. 11; viz., previous discussion of the meandering ITCZ). Modeling experiments provide reasonable evidence for low temperatures and dryness in the lowlands, but there is a wide range in the values (R. S. Webb, pers. comm., 2005). Anhuf et al. (2006) suggest that the humid forests of the Amazon Basin were reduced to about 54% of their present extent at the LGM (84% for African rain forests). Another consideration is that envisioning lowland Neotropical rain forest existing across the basin throughout the Quaternary, in light of the shifting balance of evidence in favor of significant coolness and dryness, and while accepting Davis' (1986) view that plant formations and associations are never permanent, is requiring increasing agility.

There are also recent molecular data interpreted as evidence that dryness had an effect on the rain forest. Wüster et al. (2005a, p. 1095) used three mitochondrial genes to infer the phylogeography of the Neotropical rattlesnake *Crotalus durissus*, and conclude that "the phylogeographical pattern is consistent with gradual dispersal along the Central American Isthmus, followed by more rapid dispersal into and across South America after the uplift of the Isthmus of Panamá. Low sequence divergence between populations from north and south of the Amazonian rainforest is consistent with mid-Pleistocene divergence, approximately 1.1 million years ago (Ma). This suggests that the Amazonian rainforests must have become fragmented or at least shrunk considerably during that period, lending support to the Pleistocene refugia theory as an important cause of distribution patterns, if not necessarily speciation, in Amazonian forest organisms." Gosling and Bush (2005) note the heterogeneity of the rain forest and the changes in composition during the Quaternary and question the use of *Crotalus durissus* to determine rain forest fragmentation, to which Wüster et al. (2005b, p. 3619) reply, "We reject these doubts, and maintain that the presence of *C. durissus* on both sides of the Amazon Basin does represent evidence of profound changes in the distribution of rainforests in the Pleistocene and cannot be explained by relatively minor changes in rainforest community composition." In their review of the Amazonian rain forest at

the LGM, Anhuf et al. (2006, p. 518) conclude that "the point of view that claims that the Amazon lowland forests were not replaced by savanna during the LGM can no longer be supported by the data."

One consequence of the current trend in global warming may be to provide an unfortunate demonstration of the effects of drying on tropical rain forest ecosystems:

> "Drought hit the Amazon last year, with devastating results. Rivers fell, fish rotted and routes to schools and hospitals were cut off. Now studies of the dry spell suggest that such conditions could become increasingly common. The drought first caught scientists' interest because its cause was unusual. Dry spells in the Amazon usually occur in El Niño years, when warm water off the Pacific coast of South America sets up a pattern of circulating air that inhibits rainfall in the Amazon. But last year was not an El Niño year. Instead, the drought was caused by a circulation pattern powered by warm seas in the Atlantic—the same phenomenon responsible for last year's unusually intense Atlantic hurricane season. The result was a dry spell that hit particularly hard in the western Amazon, a region that normally has more rainfall than other parts of the forest. The media quickly blamed global warming [and] results from other studies suggest that the Amazon could have more such events in the future." (Schiermeier, 2006, p. 726)

One of these studies indicated such droughts could destroy up to 65% of the rain forest cover by 2090 (Cox et al., 2004), possibly through the death of large trees and increased fires, with a significant increase of 0.5 billion tons of carbon into the atmosphere. If such events cannot be prevented, the next generation may witness whether drying allows a continuous cover of rain forest to persist or, along with other factors, contributes to the expansion of dry communities, with parcels of rain forest occupying or persisting longer in some of the wettest areas now designated as potential refugia.

Cautionary notes and opinions 7 (Refugia):

Views about past environments in the lowland Neotropics have progressed from (1) it was not significantly cooler during the glacial maxima, (2) it was cooler but not dry, to (3) it was cooler and dry enough to cause change in the extent and composition of the rain forest, acknowledging the dynamic nature of communities over time, but not enough to disrupt it and allow expansion of dry forest, savanna, and/or grassland into the basin, thus refuting the refugium concept. The present assessment of the combined evidence is that the Quaternary environmental changes disrupted the lowland tropical rain forest or, more relevant for diversification, they isolated some component breeding populations, into segments that can be regarded as refugia existing where moist conditions were perpetuated during periods of dryness. The dry areas were more than just around the periphery of the forest, and the wet areas included the confluency of major rivers, slopes of the Andes Mountains, deep river valleys, gallery forest environments (Meave et al., 1991; Pennington et al., 2000), and possibly in super-wet areas where the elbow of the Andes Mountains creates even greater avected precipitation (Killeen et al., 2007). One difference from the original version is that these are not necessarily the same refugia as proposed by Haffer and others 40 years ago (Panama uplands; Lake Valencia, Chapter 7). Another is the multi-factored complex of causes now recognized as driving vegetation change in the Amazon Basin. Also, a factor not often emphasized is that for a refugium mechanism to operate in the lowland tropical rain forest, it is not necessary for the intervening areas to be desert, caatingas, cerrado, savanna, or grassland. It is only necessary that the surrounding vegetation types be drier than the lowland tropical rain forest, and these types may include moist, tropical deciduous, or dry tropical forest. This is quite different from the constraint that intervening areas must be arid or extremely arid. Collectively, modifications such as these are expected in an idea allowed to evolve as new information accumulates.

Spore and pollen diagrams provide impressions of vegetation change, like the summary profile in Fig. 8.43 from Carajás in eastern Amazonia that shows alternating forest and savanna vegetation. Others, like the Sum Arboreal column of Fig. 8.45 from Lake Pata in northwestern Brazil, show essentially continuous forest throughout the ~40-Kyr interval. I believe these diagrams accurately depict a general scenario of climate and vegetation history at different places in the Amazon Basin during the Quaternary. Overall, the independent evidence for dryness makes it no longer tenable to maintain that the lowland tropical rain forest was not significantly impacted throughout the late Neogene and the 2.6 Ma years of the Quaternary. In my opinion, the balance of evidence has shifted, and trying to envision a continuous cover of rain forest, while accepting the obvious dynamic nature of the community, has now become more difficult than accepting the refugium concept as revised by the balance of recent information.

NOTES

1. Geographic information system (GIS) is a system of hardware, software, and procedures for capturing, storing, checking, integrating, manipulating, analyzing, and displaying data that are spatially referenced to the Earth. These data may include the status and changes in the physical features and vegetation of the Earth, and recording of collection data. Images are captured by satellites, retrieved by Global Positioning System (GPS) receivers, entered into a computer, and studied or printed out in the laboratory or directly in the field. An important consequence of the technology has been to identify an unexpectedly large number of old landslides and river meanderings (ancient channels) that document the dynamic history of the lowland South American landscape.

2. "Phylogeography is a field of study concerned with the principles and processes governing the geographic distributions of genealogical lineages, especially those within and among closely related species" (Avise, 2000, p. 3); viz., the spatial distribution of phylogenetically meaningful traits and lineages.

REFERENCES

Ab'Saber, A. N. 1982. The paleoclimate and paleoecology of Brazilian Amazonia. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 41–59.

Absy, M. L. 1982. Quaternary palynological studies in the Amazon Basin. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 67–73.

——— and T. van der Hammen. 1976. Some palaeoecological data from Rondônia, southern part of the Amazon Basin. Acta Amazonica 6: 293–299.

Adams, C. G., D. E. Lee, and B. R. Rosen. 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 77: 289–313.

Aeschbach-Hertig, W., F. Peeters, U. Beyerle, and R. Kipfer. 2000. Palaeotemperature reconstruction from noble gases in ground water taking into account equilibration with entrapped air. Nature 405: 1040–1044.

Anderson, C. L., K. Bremer, and E. M. Friis. 2005. Dating phylogenetically basal eudicots using *rbcL* sequences and multiple fossil reference points. Amer. J. Bot. 92: 1737–1748.

Anhuf, D. et al. (+ 12 authors). 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239: 510–527.

Arimoto, R. 2001. Eolian dust and climate: Relationships to sources, tropospheric chemistry, transport and deposition. Earth-Sci. Rev. 54: 29–42.

Ashton, P. S. 1969. Speciation among tropical forest trees: Some deductions in the light of recent evidence. *In:* R. H. Lowe-McConnell (ed.), Speciation in Tropical Environments. Academic Press, London. pp. 155–196.

Avise, J. C. 2000. Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, MA.

———. 2004. What is the field of biogeography, and where is it going? Taxon 53: 893–898.

Axelrod, D. I. 1975. Evolution and biogeography of the Madrean–Tethyan sclerophyll vegetation. Ann. Missouri Bot. Gard. 62: 280–334.

———. 1984. An interpretation of Cretaceous and Tertiary biota in polar regions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 45: 105–147.

Barreda, V. D. 1997a. Palynomorph assemblage of the Chenque Formation, late Oligocene?–Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Parts 1–4. Ameghiniana 34: 69–80, 81–92, 131–144, 145–154.

———. 1997b. Palinoestratigrafía de la Formación San Julián en el área de Playa La Mina (Provincia de Santa Cruz), Oligoceno de la Cuenca Austral. Ameghiniana 34: 283–294.

——— and M. Caccavari. 1992. Mimosoideae (Leguminosae) occurrences in the early Miocene of Patagonia (Argentina). Palaeogeogr. Palaeoclimatol. Palaeoecol. 94: 243–252.

——— and L. Palazzesi. 2005. Patagonian vegetation turnovers during the Paleogene–early Neogene: Origin of arid-adapted floras. Abstract, XVI Congreso Geólogico Argentino (La Plata, November 2005). 1 p.

Bartlett, A. S. and E. S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change). *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 203–299.

Baum, D. A., R. Small, and J. Wendel. 1998. Biogeography and floral evolution of baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. Syst. Biol. 47: 181–207.

Behling, H. and H. Hooghiemstra. 1998. Holocene history of the Chocó rain forest from Laguna Piusbi, southern Pacific lowlands of Colombia. Quatern. Res. 50: 300–308.

Bengtsson, L. 2001. Hurricane threats. Science 293: 440–441.

Berry, E. W. 1921. Tertiary fossil plants from Costa Rica. Proc. U. S. Natl. Mus. 59: 169–185.

Betancourt, J. L., C. Latorre, J. A. Rech, J. Quade, and K. A. Rylander. 2000. A 22,000-year record of monsoonal precipitation from northern Chile's Atacama Desert. Science 289: 1542–1546.

BioBriefs. 1991. Amazon rain forest sucks up Saharan soil. BioScience 41: 439.

Birkenmajer, J. 1990. Geochronology and climatostratigraphy of Tertiary glacial and interglacial succession on King George Island, South Shetland Islands (West Antarctica). *In:* H. Miller (ed.), Zentralblatt für Geologie und Paleontologie Teil I, Workshop on Antarctic Geochronology. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. pp. 141–151.

Bohm, B. A. and T. F. Stuessy. 2001. Flavonoids of the Sunflower Family (Asteraceae). Springer Verlag, Berlin.

Bremer, K. 1994. Asteraceae: Cladistics and Classification. Timber Press, Portland, OR.

Brown, K. S., Jr. 2005. Geologic, evolutionary, and ecological bases of the diversification of Neotropical butterflies: Implications for conservation. *In:* E. Bermingham, C. W. Dick, and C. Moritz (eds.), Tropical Rainforests: Past, Present, and Future. University of Chicago Press, Chicago. pp. 166–201.

———, P. M. Sheppard, and J. R. G. Turner. 1974. Quaternary refugia in tropical America: Evidence from race formation in *Heliconius* butterflies. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 187: 369–378.

Burbridge, R. E., F. E. Mayle, and T. J. Killeen. 2004. Fifty-thousand-year vegetation and climate history of Noel

Kempff Mercado National Park, Bolivian Amazon. Quatern. Res. 61: 215–230.

Burnham, R. J. 1995. A new species of winged fruit from the Miocene of Ecuador: *Tipuana ecuadoriana* (Leguminosae). Amer. J. Bot. 82: 1599–1607.

——— and A. Graham. 1999. The history of Neotropical vegetation: New developments and status. Ann. Missouri Bot. Gard. 86: 546–589.

——— and K. R. Johnson. 2004. South American palaeobotany and the origins of Neotropical rainforests. *In:* R. T. Pennington, Q. C. B. Cronk, and J. A. Richardson (eds.), Plant Phylogeny and the Origin of Major Biomes. Philos. Trans., Ser. B 359: 1595–1610.

Bush, M. B. 2002. On the interpretation of fossil Poaceae in the lowland humid Neotropics. Palaeogeogr. Palaeoclimatol. Palaeoecol. 177: 5–17.

——— and P. A. Colinvaux. 1990. A pollen record of a complete glacial cycle from lowland Panama. J. Veg. Sci. 1: 105–118.

———, ———, M. C. Wiemann, D. R. Piperno, and K.-b. Liu. 1990. Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. Quatern. Res. 34: 330–345.

———, P. E. De Oliveira, P. A. Colinvaux, M. C. Miller, and J. E. Moreno. 2004. Amazonian paleoecological histories: One hill, three watersheds. Palaeogeogr. Palaeoclimatol. Palaeoecol. 214: 359–393.

———, D. R. Piperno, and P. A. Colinvaux. 1989. A 6,000-year history of Amazonian maize cultivation. Nature 340: 303–305.

Caccavari, M. A. 1996. Analysis of the South American fossil pollen record of Mimosoideae (Leguminosae). Rev. Palaeobot. Palynol. 94: 123–135.

——— and L. M. Anzotegui. 1987. Polen de Mimosoideae (Leguminosae) de la Formación Ituzaingó, Plioceno superior de Corrientes, Argentina. IV Congreso Latinoamericano de Paleontologia, Bolivia 1: 443–458.

——— and V. Barreda. 2000. A new calymmate mimosoid polyad from the Miocene of Argentina. Rev. Palaeobot. Palynol. 109: 197–203.

Cadée, G. C. 1998. Darwin on dust at sea. PAGES News Int. Paleosci. Community 6: 16.

Cain, M. L., R. Nathan, and S. A. Levin (coordinating/guest eds.). 2003. Long-distance dispersal. Ecology 84: 1943–2020.

Campbell, K. E., Jr. 1982. Late Pleistocene events along the coastal plain of northwestern South America. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 423–440.

Cantrill, D. J. and I. Poole. 2005. Taxonomic turnover and abundance in Cretaceous to Tertiary wood floras of Antarctica: Implications for changes in forest ecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 215: 205–219.

Chanderbali, A. S., H. van der Werff, and S. S. Renner. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. Ann. Missouri Bot. Gard. 88: 104–134.

Clapperton, C. 1993. Quaternary Geology and Geomorphology of South America. Elsevier Science Publishers, Amsterdam.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.). 2001. Dispersal. Oxford University Press, Oxford, U.K.

Coleman, M., A. Liston, J. W. Kadereit, and R. J. Abbott. 2003. Repeat intercontinental dispersal and Pleistocene speciation in disjunct Mediterranean and desert *Senecio* (Asteraceae). Amer. J. Bot. 90: 1446–1454.

Colinvaux, P. A. 1997. The ice-age Amazon and the problem of diversity. NWO Huygens Lecture, 1997, The Hague, The Netherlands, Organization for Scientific Research (NWO), pp. 7–30. [Reprinted in Colinvaux et al., 1999.]

———. 2005. The Pleistocene vector of Neotropical diversity. *In:* E. Bermingham, C. W. Dick, and C. Moritz (eds.), Tropical Rainforests: Past, Present, and Future. University of Chicago Press, Chicago. pp. 78–106.

———, P. E. De Oliveira, and M. B. Bush. 2000. Amazonian and Neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. Quatern. Sci. Rev. 19: 141–169.

———, ———, and J. E. Moreno Patiño. 1999. Amazon Pollen Manual and Atlas. Harwood Academic Publishers, Amsterdam.

———, ———, ———, M. C. Miller, and M. B. Bush. 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. Science 274: 85–88.

———, G. Irion, M. E. Räsänen, M. B. Bush, and J. A. S. Nunes de Mello. 2001. A paradigm to be discarded: Geological and palaeoecological data falsify the Haffer & Prance refuge hypothesis of Amazonian speciation. Amazonia 16: 609–646.

——— and K.-b. Liu. 1987. The Late-Quaternary climate of the western Amazon Basin. *In:* W. H. Berger and L. D. Labeyrie (eds.), Abrupt Climatic Change. D. Reidel Publishing Company, Dordrecht, The Netherlands. pp. 113–122.

Conti, E., T. Eriksson, J. Schönenberger, K. J. Sytsma, and D. A. Baum. 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: Evidence from phylogeny and molecular dating. Evolution 56: 1931–1942.

Corner, E. J. H. 1958. The evolution of tropical forest. *In:* J. Huxley, A. C. Hardy, and E. B. Ford (eds.), Evolution as a Process. Allen and Unwin, London. pp. 34–46.

Cox, P. M. et al. (+ 5 authors). 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. Theor. Appl. Climatol. 78: 137–156.

Coxall, H. K., P. A. Wilson, H. Pälike, C. H. Lear, and J. Backman. 2005. Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. Nature 433: 53–57.

Croizat, L., G. Nelson, and D. E. Rosen. 1974. Centers of origin and related concepts. Syst. Zool. 23: 265–287.

Darlington, P. J., Jr. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol. 13: 274–300.

———. 1948. The geographical distribution of cold-blooded vertebrates. Quart. Rev. Biol. 23: 1–26, 105–123.

———. 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley & Sons, New York.

———. 1964. Drifting continents and late Paleozoic geography. Proc. Natl. Acad. Sci. U.S.A. 52: 1084–1091.

Da Silva, M. N. F. and J. L. Patton. 1993. Amazonian phylogeography: mtDNA sequence variation in arboreal echimyid rodents (Caviomorpha). Molec. Phylogen. Evol. 2: 243–255.

Davis, C. C., C. D. Bell, P. W. Fritsch, and S. Mathews. 2002. Phylogeny of *Acridocarpus–Brachylophon* (Malpighiaceae): Implications for Tertiary tropical floras and Afro-Asian biogeography. Evolution 56: 2395–2405.

———, P. W. Fritsch, C. D. Bell, and S. Mathews. 2004. High-latitude Tertiary migrations of an exclusively tropical clade: Evidence from Malpighiaceae. Int. J. Pl. Sci. 165 (Suppl.): S107–S121.

Davis, M. B. (ed.). 1986. Vegetation–climate equilibrium. Vegetatio 67: 1–141.

Deep Time Project. 2002 et seq. Deep time-dating divergences. http://www.flmnh.edu/deeptime/datingdivergences.html.

Deevey, E. S. 1949. Biogeography of the Pleistocene. Geol. Soc. Amer. Bull. 60: 1315–1416.

de Lima, M. R. and E. da Silva Amador. 1985. Analise palinológica de sedimentos da Formação Resende, Terciário do estado do Rio de Janeiro, Brasil. Dept. Nac. Prod. Mineral. Ser. Geol. 27: 371–378.

De Oliveira, P. E. 1992. A palynological record of late Quaternary vegetational and climatic change in southeastern Brazil. Ph.D. Dissertation, The Ohio State University, Columbus.

de Queiroz, A. 2005. The resurrection of oceanic dispersal in historical biogeography. Trends Ecol. Evol. 20: 68–73.

Dettmann, M. E. and H. T. Clifford. 1992. Phylogeny and biogeography of *Ruffordia*, *Mohria* and *Anemia* (Schizaeaceae) and *Ceratopteris* (Pteridaceae): Evidence from in situ and dispersed spores. Alcheringa 16: 269–314.

———, D. T. Pocknall, E. J. Romero, and M. del C. Zamaloa. 1990. *Nothofagidites* Erdtman ex Potonié, 1960; a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (southern beech). New Zealand Geol. Surv. Paleontol. Bull. 60: 1–79.

DeVore, M. L. and T. F. Stuessy. 1995. The place and time of origin of the Asteraceae, with additional comments on the Calyceraceae and Goodeniaceae. *In:* D. J. N. Hind, C. Jeffrey, and G. V. Pope (eds.), Advances in Compositae Systematics. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 23–40.

Dick, C. W., K. Abdul-Salim, and E. Bermingham. 2003. Molecular systematic analysis reveals cryptic Tertiary diversification of a widespread tropical rain forest tree. Amer. Naturalist 162: 691–703. [*Symphonia globulifera*.]

Dilcher, D. L. 1973. A paleoclimatic interpretation of the Eocene floras of southeastern North America. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 39–59.

Dingle, H. 1996. Migration: The Biology of Life on the Move. Oxford University Press, Oxford, U.K.

Dobzhansky, T. 1950. Evolution in the tropics. Amer. Sci. 38: 209–221.

Douady, C. J., F. Catzeflis, J. Raman, M. S. Springer, and M. J. Stanhope. 2003. The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews). Proc. Natl. Acad. Sci. U.S.A. 100: 8325–8330.

Drinnan, A. N., P. R. Crane, E. M. Friis, and K. R. Pedersen. 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. Bot. Gaz. 151: 370–384.

Ebach, M. C. (forum ed.). 2004. Forum on biogeography: Introduction. Taxon 53: 889–891.

Eckert, A. J. and B. D. Hall. 2006. Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): Phylogenetic tests of fossil-based hypotheses. Molec. Phylogen. Evol. 40: 166–182.

Elsner, J. B. 2007. Climatology: Tempests in time. Nature 447: 647–649.

Erkens, R. H. J., L. W. Chatrou, J. W. Maas, T. van der Niet, and V. Savolainen. 2007. A rapid diversification of rainforest trees (*Guatteria*; Annonaceae) following dispersal from Central into South America. Molec. Phylogen. Evol. 44: 399–411.

Ferraz-Vicentini, K. R. and M. L. Salgado-Labouriau. 1996. Palynological analysis of a palm swamp in central Brazil. J. S. Amer. Earth Sci. 9: 207–219.

Figueroa, N. and C. A. Nobre. 1990. Precipitation distribution over central and western tropical South America. Climanálise 5: 36–42.

Filho, A. C., D. Schwartz, S. H. Tatumi, and T. Rosique. 2002. Amazonian paleodunes provide evidence for drier climate phases during the late Pleistocene–Holocene. Quatern. Res. 58: 205–209.

Flannery, T. 2001. The Eternal Frontier: An Ecological History of North America and Its Peoples. Atlantic Monthly Press, New York.

Flenley, J. R. 2005. Palynological richness and the tropical rain forest. *In:* E. Bermingham, C. W. Dick, and C. Moritz (eds.), Tropical Rainforests: Past, Present, and Future. University of Chicago Press, Chicago. pp. 72–77.

Forest, F. et al. (+ 5 authors). 2005. Teasing apart molecular-versus fossil-based error estimates when dating phylogenetic trees: A case study in the birch family (Betulaceae). Syst. Bot. 30: 118–133.

Fortey, R. 2004. Earth: An Intimate History. Alfred A. Knopf,

New York.

Friis, E. M., K. R. Pedersen, and P. R. Crane. 2006. Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 232: 251–293.

Garrison, V. H. et al. (+ 9 authors). 2003. African and Asian dust: From desert soils to coral reefs. BioScience 53: 469–480.

Gee, C. T. 1990. On the fossil occurrences of the mangrove palm *Nypa*. Proc. Symp. Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary (Prague, 1989): 315–319.

———. 1992. A new mangrove flora from the middle Eocene of Texas. Abstract, Amer. J. Bot. 79: 105–106.

Geisler, F. 1945. A study of pollen grains of thirty-two species of grasses. Butler Univ. Bot. Stud. 7: 1–7.

Gentry, A. H. 1982. Phytogeographic patterns as evidence for a chocó refuge. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 112–136.

———. 1986a. Endemism in tropical vs. temperate plant communities. *In:* M. E. Soulé (ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA. pp. 153–181.

———. 1986b. Species richness and floristic composition of chocó region plant communities. Caldasia 15: 71–91.

———. 1993. A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru), with Supplementary Notes on Herbaceous Taxa. University of Chicago Press, Chicago.

George, W. and R. Lavocat. 1993. The Africa–South America Connection. Clarendon Press, Oxford, U.K.

Germeraad, J. H., C. A. Hopping, and J. Muller. 1968. Palynology of Tertiary sediments from tropical areas. Rev. Palaeobot. Palynol. 6: 189–348.

Gibbons, A. 1996. On the many origins of species. Science 273: 1496–1499.

Giles, J. 2005. The dustiest place on Earth. Nature 434: 816–819.

———. 2006. The outlook for Amazonia is dry. Nature 442: 726–727.

Givnish, T. J. et al. (+ 5 authors). 2000. Molecular evolution, adaptive radiation, and geographical diversification in the amphiatlantic family Rapateaceae: Evidence from *ndh*F sequences and morphology. Evolution 54: 1915–1937.

——— and S. S. Renner. 2004. Tropical intercontinental disjunctions: Gondwana breakup, immigration from the boreotropics, and transoceanic dispersal. Int. J. Pl. Sci. 165: S1–S6.

Goldblatt, P. (ed.). 1993. Biological Relationships between Africa and South America. Yale University Press, New Haven, CT.

Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nuñez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: Causes and implications. Science 293: 474–479.

González-Guzmán, A. E. 1967. A palynological study of the upper Los Cuervos and Mirador formations (lower and middle Eocene; Tibú area, Colombia). E. J. Brill, Leiden, The Netherlands.

Gosling, W. D. and M. B. Bush. 2005. A biogeographic comment on: Wüster et al. (2005) Tracing an invasion: landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). Molec. Ecol. 14: 3615–3617.

———, F. E. Mayle, N. J. Tate, and T. J. Killeen. 2005. Modern pollen-rain characteristics of tall *terre firme* moist evergreen forest, southern Amazonia. Quatern. Res. 64: 284–297.

Graham, A. 1962. *Ficus ceratops* Knowlton and its affinities with the living genus *Guarea*. J. Paleontol. 36: 521–523.

———. 1973. History of the arborescent temperate element in the northern Latin American biota. *In:* A. Graham (ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam. pp. 301–314.

———. 1976a. Studies in Neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Garden 63: 787–842. [Now middle Pliocene.]

———. 1976b. Late Cenozoic evolution of tropical lowland vegetation in Veracruz, Mexico. Evolution 29: 723–735.

———. 1985. Studies in Neotropical paleobotany. IV. The Eocene communities of Panama. Ann. Missouri Bot. Gard. 72: 504–534.

———. 1987. Miocene communities and paleoenvironments of southern Costa Rica. Amer. J. Bot. 74: 1501–1518.

———. 1991a. Studies in Neotropical paleobotany. VIII. The Pliocene communities of Panama—Introduction and ferns, gymnosperms, and angiosperms (monocots). Ann. Missouri Bot. Gard. 78: 190–200.

———. 1991b. Studies in Neotropical paleobotany. IX. The Pliocene communities of Panama—Angiosperms (dicots). Ann. Missouri Bot. Gard. 78: 201–223.

———. 1991c. Studies in Neotropical paleobotany. X. The Pliocene communities of Panama—Composition, numerical representations, and paleocommunity paleoenvironmental reconstructions. Ann. Missouri Bot. Gard. 78: 465–475.

———. 1992a. Utilization of the isthmian landbridge during the Cenozoic—Paleobotanical evidence for timing and the selective influence of altitudes and climate. Rev. Palaeobot. Palynol. 72: 119–128.

———. 1992b. The current status of the legume fossil record in the Caribbean region. *In:* P. S. Herendeen and D. L. Dilcher (eds.), Advances in Legume Systematics: 4. The Fossil Record. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 161–167.

———. 1994. Neotropical Eocene coastal floras and $^{18}O/^{16}O$-estimated warmer vs. cooler equatorial waters. Amer. J. Bot. 81: 301–306.

———. 1995. Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. Biotropica 27:

20–27.
———. 1996. A contribution to the geologic history of the Compositae. *In:* D. J. N. Hind and H. J. Beentje (eds.). Compositae: Systematics. Proceedings of the International Compositae Conference (Kew, 1994), Vol. 1. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 123–140.
———. 1997. Neotropical plant dynamics during the Cenozoic—Diversification, and the ordering of evolutionary and speciation processes. Syst. Bot. 22: 139–150.
———. 1998. Studies in Neotropical paleobotany. XI. Late Tertiary vegetation and environments of southeastern Guatemala: Palynofloras from the Mio–Pliocene Padre Miguel and the Pliocene Herrería Formation. Amer. J. Bot. 85: 1409–1425.
———. 1999. Late Cretaceous and Cenozoic History of North American Vegetation (North of Mexico). Oxford University Press, Oxford, U.K.
———. 2003a. Historical phytogeography of the Greater Antilles. Brittonia 55: 357–383.
———. 2003b. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Syst. Bot. 28: 378–386.
———. 2005. Interfacing paleobotanical with molecular/systematic data in biogeography. Abstract, Symposium—The impact of plant dispersal on biogeography: Current understanding and prospects. XVII International Botanical Congress (Vienna, Austria, July 2005). 1 p.
——— (organizer). 2006a. Latin American Biogeography—Causes and Effects. Ann. Missouri Bot. Gard. 93: 173–358.
———. 2006b. Modern processes and historical factors in the origin of the African element in Latin America. *In:* A. Graham (organizer), Latin American Biogeography—Causes and Effects. Ann. Missouri Bot. Gard. 93: 325–339.
———. 2006c. Paleobotanical evidence and molecular data in reconstructing the historical phytogeography of Rhizophoraceae. *In:* A. Graham (organizer), Latin American Biogeography—Causes and Effects. Ann. Missouri Bot. Gard. 93: 325–334.
———. 2009. Fossil record of the Rubiaceae. Ann. Missouri Bot. Gard. 96: 90–108.
——— and G. Barker. 1981. Palynology and tribal classification in the Caesalpinioideae. *In:* R. M. Polhill and P. H. Raven (eds.), Advances in Legume Systematics. HMSO, London. pp. 801–834.
——— and D. L. Dilcher. 1998. Studies in Neotropical paleobotany. XII. A palynoflora from the Pliocene Río Banano Formation of Costa Rica and the Neogene vegetation of Mesoamerica. Amer. J. Bot. 85: 1426–1438.
——— et al. (+ 5 authors). 1985. Palynology and systematics of the Lythraceae. I. Introduction and genera *Adenaria* through *Ginoria*. Amer. J. Bot. 72: 1012–1031.
——— et al. (+ 5 authors). 1987. Palynology and systematics of the Lythraceae. II. Genera *Haitia* through *Peplis*. Amer. J. Bot. 74: 829–850.
———, S. A. Graham, J. W. Nowicke, V. Patel, and S. Lee. 1990. Palynology and systematics of the Lythraceae. III. Genera *Physocalymma* through *Woodfordia*, addenda, and conclusions. Amer. J. Bot. 77: 159–177.
Graham, S. A. 2002. Phylogenetic relationships and biogeography of the endemic Caribbean genera *Crenea*, *Ginoria*, and *Haitia* (Lythraceae). Caribbean J. Sci. 38: 195–204.
———, J. Hall, K. Sytsma, and S.-h. Shi. 2005. Phylogenetic analysis of the Lythraceae based on four gene regions and morphology. Int. J. Pl. Sci. 166: 995–1017.
Gray, W. M. 1990. Strong association between West African rainfall and U.S. landfall of intense hurricanes. Science 249: 1251–1256.
Griffin, D. W., C. A. Kellogg, V. H. Garrison, and E. A. Shinn. 2002. The global transport of dust. Amer. Sci. 90: 228–235.
Guilderson, T. P., R. G. Fairbanks, and J. L. Rubenstone. 1994. Tropical temperature variations since 20,000 years ago: Modulating interhemispheric climate change. Science 263: 663–268.
Guillaumet, J.-L. 1989. Les massifs forestiers intertropicaux humides Africain et Américain: Analogies et différences. Bull. Soc. Bot. France 136: 59–65.
Haffer, J. 1969. Speciation in Amazonia forest birds. Science 165: 131–137.
———. 1970. Geologic, climatic history and zoogeographic significance of the Urabá region in northwestern Colombia. Caldasia 10: 603–636.
———. 1974. Avian Speciation in Tropical South America. Publ. Nuttall Ornithological Club No. 14. Cambridge, MA.
———. 1982. General aspects of the refuge theory. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 6–24.
Hammel, B. E. and N. A. Zamora. 1993. *Ruptiliocarpon* (Lepidobotryaceae): A new arborescent genus and tropical American link to Africa, with a reconsideration of the family. Novon 3: 408–417.
Harris, W. K. 1974. Palynology of cores from DSDP sites 327, 328, and 330, South Atlantic Ocean. Initial Reports of the Deep Sea Drilling Project 36: 761–775.
Harrison, S. P., K. E. Kohfeld, C. Roelandt, and T. Claquin. 2001. The role of dust in climate changes today, at the last glacial maximum and in the future. Earth-Sci. Rev. 54: 43–80.
Hedges, S. B. 1996. Historical biogeography of West Indian vertebrates. Ann. Rev. Ecol. Syst. 27: 163–196.
Heine, K. 1994. The Mera site revisited: Ice-age Amazonia in the light of new evidence. Quatern. Int. 21: 113–119.
———. 2000. Tropical South America during the Last Glacial Maximum: Evidence from glacial, periglacial and fluvial records. Quatern. Int. 72: 7–21.
Heinicke, M. P., W. E. Duellman, and S. B. Hedges. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. Proc. Natl. Acad. Sci. U.S.A.

104: 10092–10097.
Herendeen, P. S., W. L. Crepet, and D. L. Dilcher. 1992. The fossil history of the Leguminosae: Phylogenetic and biogeographic implications. *In:* P. S. Herendeen and D. L. Dilcher (eds.), Advances in Legume Systematics: Part 4. The Fossil Record. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 303–316.
Herngreen, G. F. W. and H. Duenas Jiménez. 1990. Dating of the Cretaceous Une Formation, Colombia and the relationship with the Albian–Cenomanian African–South American microfloral province. Rev. Palaeobot. Palynol. 66: 345–359.
Heyer, W. R. and L. R. Maxson. 1982. Distributions, relationships, and zoogeography of lowland frogs: The *Leptodactylus* complex in South America, with special reference to Amazonia. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 375–388.
Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17–33.
———. 1979. A revised classification of the architecture of dicotyledonous leaves. *In:* C. R. Metcalfe and L. Chalk (eds.), Anatomy of the Dicotyledons. Vol. 1. Clarendon Press, Oxford, U.K. pp. 25–39.
Higgins, S. I., R. Nathan, and M. L. Cain. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84: 1945–1956.
Hill, R. S. 2001. Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): The contribution of the fossil record. Austral. J. Bot. 49: 321–332.
——— and M. E. Dettmann. 1996. Origin and diversification of the genus *Nothofagus*. *In:* T. T. Veblen, R. S. Hill, and J. Read (eds.), The Ecology and Biogeography of *Nothofagus* Forest. Yale University Press, New Haven, CT. pp. 11–24.
——— and J. Read. 1991. A revised infrageneric classification of *Nothofagus* (Fagaceae). J. Linn. Soc., Bot. 105: 37–72.
Hinojosa, L. F. and C. Villagrán. 2005. Did South America mixed paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic? Palaeogeogr. Palaeoclimatol. Palaeoecol. 217: 1–23.
Hooghiemstra, H. 1984. Vegetational and climatic history of the High Plain of Bogotá: A continuous record of the last 3.5 million years. Diss. Bot. 79: 1–368.
———. 1989. Quaternary and upper-Pliocene glaciations and forest development in the tropical Andes: Evidence from a long high-resolution pollen record from the sedimentary basin of Bogotá, Colombia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 72: 11–26.
———. 1994. Pliocene–Quaternary floral migration, evolution of northern Andean ecosystems and climatic change: Implications from the closure of the Panamanian isthmus. Profil (Institut für Geologie und Paläontologie, Universität Stuttgart) 7: 413–425.
——— and E. T. H. Ran. 1994. Late and middle Pleistocene climatic change and forest development in Colombia: Pollen record Funza II (1–158 m core interval). Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 211–246.
——— and G. Sarmiento. 1991. New long continental pollen record from a tropical intermontane basin: Late Pliocene and Pleistocene history from a 540 m core. Episodes 14: 107–115.
——— and T. van der Hammen. 1998. Neogene and Quaternary development of the Neotropical rain forest: The forest refugia hypothesis, and a literature overview. Earth-Sci. Rev. 44: 147–183.
Hoorn, C. 1994. Miocene palynostratigraphy and paleoenvironments of northwestern Amazonia: Evidence for marine incursions and the influence of Andean tectonics. Ph.D. Dissertation, University of Amsterdam, Amsterdam.
Hoyos, C. D., P. A. Agudelo, P. J. Webster, and J. A. Curry. 2006. Deconvolution of the factors contributing to the increase in global hurricane intensity. Science 312: 94–97.
Huang, J. L. and R. A. Prince. 2003. Estimation of the age of extant *Ephedra* using chloroplast *rbc*L sequence data. Molec. Biol. Evol. 20: 435–440.
Huber, B. T., K. G. MacLeod, and S. L. Wing (eds.). 2000. Warm Climates in Earth History. Cambridge University Press, Cambridge, U.K.
Hueber, F. M. and J. Langenheim. 1986. Dominican amber tree had African ancestors. Geotimes 31: 8–10.
Huertas-G., G. 1977. Una Melastomatácea fósil del Terciario carbonifera de Antioquia (Eoceno). Caldasia 12: 35–39.
Iriondo, M. 1999. Climatic changes in the South American plains: Records of a continent-scale oscillation. Quatern. Int. 57/58: 93–112.
——— and D. M. Kröhling. 1997. The tropical loess. Proc. 30th Int. Geol. Congr. 21: 61–77.
Iturralde-Vinent, M. A. and R. D. E. MacPhee. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. Bull. Amer. Mus. Nat. Hist. 238: 1–95.
Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314: 102–106.
Jaramillo, C. A. and D. L. Dilcher. 2001. Middle Paleogene palynology of central Colombia, South America: A study of pollen and spores from tropical latitudes. Palaeontographica, Abt. B, Paläophytol. 258: 87–213.
———, M. J. Rueda, and G. Mora. 2006. Cenozoic plant diversity in the Neotropics. Science 311: 1893–1896.
Käss, E. and M. Wink. 1997. Molecular phylogeny and phylogeography of *Lupinus* (Leguminosae) inferred from nucleotide sequences of the *rbc*L gene and ITS 1 + 2 regions of rDNA. Pl. Syst. Evol. 208: 139–167.
Kellogg, C. A. and D. W. Griffin. 2006. Aerobiology and the global transport of desert dust. Trends Ecol. Evol. 21: 638–644.
Killeen, T. J., M. Douglas, T. Consiglio, P. M. Jørgensen, and

J. Mejia. 2007. Dry spots and wet spots in the Andean hotspot. J. Biogeogr. 34: 1357–1373.

Knutson, T. R., R. E. Tuleya, and Y. Kurihara. 1998. Simulated increase of hurricane intensities in a CO_2-warmed climate. Science 279: 1018–1021.

Kohfeld, K. E. and S. P. Harrison. 2001. Dirtmap: The geological record of dust. Earth-Sci. Rev. 54: 81–114.

Koren, I. et al. (+ 6 authors). 2006. The Bodélé Depression: A single spot in the Sahara that provides most of the mineral dust to the Amazon forest. Environm. Res. Lett. I: 1–5.

Leaf Architecture Working Group. 1999. Manual of Leaf Architecture: Morphological Description and Categorization of Dicotyledonous and Net-veined Monocotyledonous Angiosperms. Smithsonian Institution, Washington, D.C.

Ledru, M.-P. 1993. Late Quaternary environmental and climatic changes in central Brazil. Quatern. Res. 39: 90–98.

Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: A theoretical perspective. Ann. Rev. Ecol. Syst. 34: 575–604.

Leyden, B. W. 1984. Guatemalan forest synthesis after Pleistocene aridity. Proc. Natl. Acad. Sci. U.S.A. 81: 4856–4859.

———. 1985. Late Quaternary aridity and Holocene moisture fluctuations in the Lake Valencia Basin, Venezuela. Ecology 66: 1279–1295.

Lichte, M. and H. Behling. 1999. Dry and cold climatic conditions in the formation of the present landscape in southeastern Brazil. Z. Geomorphol. 43: 341–358.

Linden, E. 2006. The Winds of Change: Climate, Weather, and the Destruction of Civilizations. Simon & Schuster, New York.

Liu, K.-b. and P. A. Colinvaux. 1985. Forest changes in the Amazon Basin during the Last Glacial Maximum. Nature 318: 556–557.

Lomolino, M. V. and L. R. Heaney (eds.). 2004. Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland, MA, published in association with the International Biogeography Society.

———, B. R. Riddle, and J. H. Brown. 2006. Biogeography. 3rd ed. Sinauer Associates, Sunderland, MA.

MacFadden, B. J. 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. Quatern. Res. 64: 113–124.

Macphail, M. K., N. F. Truswell, and I. R. K. Sluiter. 1994. Early Tertiary vegetation: Evidence from pollen and spores. *In:* R. S. Hill (ed.), History of the Australian Vegetation: Cretaceous to "Recent." Cambridge University Press, Cambridge, U.K. pp. 189–261.

Magallón-Puebla, S. and R. S. Cevallos-Ferriz. 1994. *Eucommia constans* n. sp. fruits from upper Cenozoic strata of Puebla, Mexico: Morphological and anatomical comparison with *Eucommia ulmoides* Oliver. Int. J. Pl. Sci. 155: 80–95.

Malcomber, S. T. 2002. Phylogeny of *Gaertnera* Lam. (Rubiaceae) based on multiple DNA markers: Evidence of a rapid radiation in a widespread, morphologically diverse genus. Evolution 56: 42–57.

Malfait, B. T. and M. G. Dinkelman. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean Plate. Geol. Soc. Amer. Bull. 83: 251–272.

Manchester, S. R. 1994. Fruits and seeds of the middle Eocene nut beds flora, Clarno Formation, Oregon. Palaeontogr. Amer. 58: 1–205.

Mandal, J. 2005. Bombacaceae pollen from the Indian Tertiary sediments and its bearing on evolution and migration. Rev. Palaeobot. Palynol. 133: 277–293.

Manos, P. S. 1997. Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequences (ITS): Taxonomic congruence with morphology and plastid sequences. Amer. J. Bot. 84: 1137–1155.

——— et al. (+ 7 authors). 2007. Phylogeny of extant and fossil Juglandaceae inferred from the integration of molecular and morphological data sets. Syst. Bot. 36: 412–430.

Markgraf, V. (ed.). 2001. Interhemispheric Climate Linkages. Academic Press, New York.

Marshall, C. R. 2006. Fossil record reveals tropics as cradle and museum. Science 314: 66–67.

Martin, H. A. 2003. The history of the family Onagraceae in Australia and its relevance to biogeography. Austral. J. Bot. 51: 585–598.

Maslin, M. A. and S. J. Burns. 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. Science 290: 2285–2287.

Mayle, F. E. and D. J. Beerling. 2004. Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 214: 11–25.

McLoughlin, S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Austral. J. Bot. 49: 271–300.

Meave, J., M. Kellman, A. MacDougall, and J. Rosales. 1991. Riparian habitats as tropical forest refugia. Global Ecol. Biogeogr. Lett. 1: 69–76.

Melendi, D. L., L. Scafati, and W. Volkeimer. 2003. Palynostratigraphy of the Paleogene Huitrera Formation in N-W Patagonia, Argentina. Neues Jahrb. Geol. Paläontol., Abh. 228: 205–273.

Miller, K. G., R. G. Fairbanks, and G. S. Mountain. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. Paleoceanography 2: 1–19.

Mohr, B. A. R. and M. E. C. Bernardes-de-Oliveira. 2004. *Endressinia brasiliana*, a magnolialean angiosperm from the Lower Cretaceous Crato Formation (Brazil). Int. J. Pl. Sci. 165: 1121–1133.

——— and H. Eklund. 2003. *Araripia florifera*, a magnoliid angiosperm from the Lower Cretaceous Crato Formation (Brazil). Rev. Palaeobot. Palynol. 126: 279–292.

——— and E. M. Friis. 2000. Early angiosperms from the Cretaceous Crato Formation (Brazil), a preliminary report. Int. J. Pl. Sci. 161(Suppl.): S155–S167.

——— and D. B. Lazarus. 1994. Paleobiogeographic distri-

bution of *Kuylisporites* and its possible relationship to the extant fern genus *Cnemidaria* (Cyatheaceae). Ann. Missouri Bot. Gard. 81: 758–767.

——— and C. Rydin. 2002. *Trifurcatia flabellata* n. gen. n. sp., a putative monocotyledon angiosperm from the Lower Cretaceous Crato Formation (Brazil). Mitt. Mus. Naturk. Berl. Geowiss. Reihe 5: 335–344.

Morell, V. 1996. Amazonian diversity: A river doesn't run through it. Science 273: 1496–1497.

Morley, R. J. 2000. Origin and Evolution of Tropical Rain Forests. John Wiley & Sons, New York.

——— and C. W. Dick. 2003. Missing fossils, molecular clocks, and the origin of the Melastomataceae. Amer. J. Bot. 90: 1638–1644.

Morton, O. 2005a. Major shifts in climate and life may rest on feats of clay. Science 309: 1320–1321.

———. 2005b. Storms bow out, but boughs remember. Science 309: 1321.

Muellner, A. N., V. Savolainen, R. Samuel, and M. W. Chase. 2006. The mahogany family "out-of-Africa": Divergence time estimation, global biogeographic patterns inferred from plastid *rbc*L DNA sequences, extant, and fossil distribution of diversity. Molec. Phylogen. Evol. 40: 236–250.

Muhs, D. R. and M. Zárate. 2001. Late Quaternary eolian records of the Americas and their paleoclimatic significance. *In:* V. Markgraf (ed.), Interhemispheric Climate Linkages. Academic Press, New York. pp. 183–216.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47: 1–142.

Muñoz, J., A. M. Felicísimo, F. Cabezas, A. R. Burgaz, and I. Martínez. 2004. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science 304: 1144–1147.

Nelson, G. 1978. From Candolle to Croizat: Comments on the history of biogeography. J. Hist. Biol. 11: 269–305.

——— and P. Y. Ladiges. 2001. Gondwana, vicariance biogeography and the New York School revisited. Austral. J. Bot. 49: 389–409.

Palma-Heldt, S. 1983. Estudio palinológico del Terciario sedimentário de Lonquimay, Provincia de Malleco, Chile. Revista Geol. Chile 18: 55–75.

Parenti, L. R. and C. J. Humphries. 2004. Historical biogeography, the natural science. Taxon 53: 899–903.

Pares Regali, M. da S., N. Uesugui, and A. da Silva Santos. 1974a. Palinología dos sedimentos Meso–Cenozoicas do Brasil (I). Bol. Tecn. Petrobras, Rio de Janeiro 17: 177–191.

———, ———, and ———. 1974b. Palinología dos sedimentos Meso–Cenozoicas do Brasil (II). Bol. Tecn. Petrobras, Rio de Janeiro, 17: 263–301.

Patton, J. L. and M. N. F. Da Silva. 1998. Rivers, refuges, and ridges: The geography of speciation of Amazonian mammals. *In:* D. Howard and S. H. Berlocher (eds.), Endless Forms: Species and Speciation. Oxford University Press, Oxford, U.K. pp. 202–213.

——— and ———. 2005. The history of Amazonian mammals: Mechanisms and timing of diversification. *In:* E. Bermingham, C. W. Dick, and C. Moritz (eds.), Tropical Rainforests: Past, Present, and Future. University of Chicago Press, Chicago. pp. 107–126.

———, ———, and J. R. Malcolm. 1994. Gene genealogy and differentiation among arboreal spiny rats (Rodentia: Echimydae) of the Amazon Basin: A test of the riverine barrier hypothesis. Evolution 48: 1314–1323.

Pearson, D. L. 1982. Historical factors and bird species richness. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 441–454.

Pennington, R. T., D. E. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. J. Biogeogr. 27: 261–273.

Penny, D. 2005. Relativity for molecular clocks. Nature 436: 183–184.

Pindell, J. L. 1994. Evolution of the Gulf of Mexico and the Caribbean. *In:* S. K. Donovan and T. A. Jackson (eds.), Caribbean Geology: An Introduction. University of the West Indies Publishers Association (UWIPA), Mona, Kingston, Jamaica. pp. 13–40.

——— and S. F. Barrett. 1990. Geological evolution of the Caribbean region; a plate-tectonic perspective. *In:* G. Dengo and J. E. Case (eds.), The Geology of North America. Vol. H. The Caribbean Region. Geological Society of America, Boulder, CO. pp. 405–432.

Polquério, M. J. F. and R. A. Nichols. 2007. Dates from the molecular clock: How wrong can we be? Trends Ecol. Evol. 22: 180–184.

Prance, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. Acta Amazonica 3: 5–28.

——— (ed.). 1982. Biological Diversification in the Tropics. Columbia University Press, New York.

Prospero, J. M. 2001. African dust in America. Geotimes (November): 24–27.

——— and P. J. Lamb. 2003. African droughts and dust transport to the Caribbean: Climate change implications. Science 302: 1024–1027.

Reid, R. P., S. N. Cary, and D. R. Ross. 1996. Late Quaternary sedimentation in the Lesser Antilles island arc. Geol. Soc. Amer. Bull. 108: 78–100.

Renner, S. S. 2005. Relaxed molecular clocks for dating historical plant dispersal events. Trends Pl. Sci. 10: 550–558.

———, G. Clausing, and K. Meyer. 2001. Historical biogeography of Melastomataceae: The roles of Tertiary migration and long-distance dispersal. Amer. J. Bot. 88: 1290–1300.

——— and T. J. Givnish (organizers). 2004. Tropical Intercontinental Disjunctions. Int. J. Pl. Sci. 165(Suppl.): S1–S138.

———, D. B. Foreman, and D. Murray. 2000. Timing transantarctic disjunctions in the Antherospermataceae (Laurales): Evidence from coding and noncoding chloroplast

sequences. Syst. Biol. 49: 579–591.
——— and K. Meyer. 2001. Melastomeae come full circle: Biogeographic reconstruction and molecular clock dating. Evolution 55: 1315–1324.
Richards, P. W. 1964. The Tropical Rain Forest. Cambridge University Press, Cambridge, U.K.
——— (with contributions by R. P. D. Walsh, I C. Baillie, and P. Greig-Smith). 1996. The Tropical Rain Forest. 2nd ed. Cambridge University Press, Cambridge, U.K.
Rohwer, J. G. 1993. Lauraceae. *In:* K. Kubitzki (ed.), The Families and Genera of Vascular Plants. II. Flowering Plants: Dicotyledons, Magnoliid, Hamamelid and Caryophyllid Families. Springer Verlag, Berlin. pp. 366–391.
Romero, E. J. 1973. Polen de "*Nothofagus*" ("*Nothofagidites*") del Cretácico y Paleoceno de Patagonia. Revista Mus. La Plata 7: 291–303.
———. 1993. South American paleofloras. *In:* P. Goldblatt (ed.), Biological Relationships between Africa and South America. Yale University Press, New Haven, CT. pp. 62–85.
——— and S. Archangelsky. 1986. Early Cretaceous angiosperm leaves from southern South America. Science 234: 1580–1582.
Rosen, D. E. 1976. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431–464.
———. 1985. Geological hierarchies and biogeographic congruence in the Caribbean. Ann. Missouri Bot. Gard 72: 636–659.
Rossetti, D. de F., P. M. de Toledo, and A. M. Góes. 2005. New geological framework for western Amazonia (Brazil) and implications for biogeography and evolution. Quatern. Res. 63: 78–89.
Rothwell, G. W. and K. C. Nixon. 2006. How does the inclusion of fossil data change our conclusions about the phylogenetic history of Euphyllophytes? Int. J. Pl. Sci. 167: 737–749.
Rutschmann, F., T. Eriksson, J. Schönenberger, and E. Conti. 2004. Did Crypteroniaceae really disperse out of India? Molecular dating evidence from *rbc*L, *ndh*F, and *rpl*16 intron sequences. Int. J. Pl. Sci. 165(Suppl.): S69–S83.
Ryan, J. C. 2001. The Caribbean gets dusted. BioScience 51: 334–338.
Rydin, C., K. R. Pedersen, and E. M. Friis. 2004. On the evolutionary history of *Ephedra*: Cretaceous fossils and extant molecules. Proc. Natl. Acad. Sci. U.S.A. 101: 16571–16576.
———, ———, P. R. Crane, and E. M. Friis. 2006. Former diversity of *Ephedra* (Gnetales): Evidence from Early Cretaceous seeds from Portugal and North America. Ann. Bot. 98: 123–140.
Salgado-Labouriau, M. L. 1982. Climatic change at the Pleistocene–Holocene boundary. *In:* G. T. Prance (ed.), Biological Diversity in the Tropics. Columbia University Press, New York. pp. 74–77.
———, M. Barberi, K. R. Ferraz-Vicentini, and M. G. Parizzi. 1998. A dry climatic event during the late Quaternary of tropical Brazil. Rev. Palaeobot. Palynol. 99: 115–129.
Schiermeier, Q. 2005. Hurricane link to climate change is hazy. Nature 437: 461.
Schmitz, B., B. Sundquist, and F. P. Andreasson (eds.). 2000. Early Paleogene Warm Climates and Biosphere Dynamics. GFF (Geologiska Föreningen), Vol. 122, Geological Society of Sweden, Stockholm.
Schwarzbach, A. E. and R. E. Ricklefs. 2000. Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. Amer. J. Bot. 87: 547–564.
——— and ———. 2001. The use of molecular data in mangrove plant research. Wetland Ecol. Managem. 9: 195–201. [Special issue: Life on the edge: Past and future of mangroves, N. C. Duke and A. E. Schwarzbach, special issue editors.]
Science. 2006. Migration and dispersal. Special section, Science 313: 775–800. [See e.g., R. Nathan, Long-distance dispersal of plants, pp. 786–788.]
Servant, M. et al. (+ 6 authors). 1993. Tropical forest changes during the late Quaternary in African and South American lowlands. Global Planet. Change 7: 25–40.
Simpson, B. B. 1997. An arid Amazon? Reply. Tree 12: 319.
Simpson, G. G. 1943. Mammals and the nature of continents. Amer. J. Sci. 241: 1–31.
Smissen, R. D., G. K. Chambers, and P. J. Garnock-Jones. 2005. Dating nodes on molecular phylogenies: Older or younger than the Earth itself? Cladistics 21: 403. [See reply, M. Heads, ibid, p. 204.]
Sole de Porta, N. 1972. Contribución a la palinología del Nivel de Lutitas y arenas (Campaniense) en Guataquí (Valle del Magdalena), Colombia. Revista Esp. Micropaleontol. 4: 225–250.
Stace, C. A. 1989. Dispersal versus vicariance: No contest! J. Biogeogr. 16: 200–201.
Stehli, F. G. and S. D. Webb (eds.). 1985. The Great American Biotic Interchange. Plenum Press, New York.
Stockey, R. A. 1977. Reproductive biology of the Cerro Cuadrado (Jurassic) fossil conifers: *Pararaucaria patagonica*. Amer. J. Bot. 64: 733–744.
———. 1978. Reproductive biology of Cerro Cuadrado fossil conifers: Ontogeny and reproductive strategies in *Araucaria mirabilis* (Spegazzini) Windhausen. Paleontographica, Abt. B, Paläophytol. 166: 1–15.
———. 1982. The Araucariaceae: An evolutionary perspective. Rev. Palaeobot. Palynol. 37: 133–154.
——— and G. W. Rothwell (eds.). 2006. Evolution of modern ferns. Special Section, Int. J. Pl. Sci. 167: 613–749.
——— and T. N. Taylor. 1978. On the structure and evolutionary relationships of the Cerro Cuadrado fossil conifer seedlings. J. Linn. Soc., Bot. 76: 161–176.
Strong, D. A. 1982. Comment (Forest Refuges: Evidence from woody angiosperms, G. T. Prance). *In:* G. T. Prance (ed.),

Biological Diversification in the Tropics. Columbia University Press, New York. pp. 157–158.

Stuart, L. C. 1954. A description of a subhumid corridor across northern Central America, with comments on its herpetofaunal indicators. Contr. Lab. Vertebrate Biol. Univ. Michigan 65: 1–26.

Stute, M. et al. (+ 7 authors). 1995. Cooling of tropical Brazil (5°C) during the Last Glacial Maximum. Science 269: 379–383.

Swenson, U. and R. S. Hill. 2001. Most parsimonious areagrams versus fossils: The case of *Nothofagus* (Nothofagaceae). Austral. J. Bot. 49: 367–376.

———, ———, and S. McLoughlin. 2001. Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. Taxon 50: 1025–1041.

Sytsma, K. J. et al. (+ 7 authors). 2004. Clades, clocks, and continents: Historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the Southern Hemisphere. Int. J. Pl. Sci. 165(Suppl.): S85–S105.

Thomas, M. F. 2000. Late Quaternary environmental changes and the alluvial record in humid tropical environments. Quatern. Int. 72: 23–36.

Toon, O. B. 2003. African dust in Florida clouds. Nature 424: 623–624.

Tremetsberger, K. et al. (+ 6 authors). 2005. Nuclear ribosomal DNA and karyotypes indicate a NW African origin of South American *Hypochaeris* (Asteraceae, Cichorieae). Molec. Phylogen. Evol. 35: 102–116.

——— et al. (+ 8 authors). 2006. AFLP phylogeny of South American species of *Hypochaeris* (Asteraceae, Lactuceae). Syst. Bot. 31: 610–626.

Trénel, P. et al. (+5 authors). 2007. Mid-Tertiary dispersal, not Gondwanan vicariance explains distribution patterns in the wax palm subfamily (Ceroxyloideae: Arecaceae). Molec. Phylogen. Evol. 45: 272–288.

Udvardy, M. D. 1969. Dynamic Zoogeography, with Special Reference to Land Mammals. Van Nostrand Reinhold, New York.

Urrego-Giraldo, L. E. 1994. Los bosques inundables del medio Caquetá (Amazonia Colombiana). Caracterización y succesión. Ph.D. Dissertation, University of Amsterdam, Amsterdam.

———. 1997. Los bosques inundables del medio Caquetá: Caracterización y succesión. Estudios en la Amazonia Colombiana/Studies on the Colombian Amazon, Vol. 14. Tropenbos–Colombia, Bogotá.

van der Hammen, T. 1961. The Quaternary climatic changes of northern South America. Ann. New York Acad. Sci. 95: 676–683.

———. 1972. Changes in vegetation and climate in the Amazon Basin and surrounding areas during the Pleistocene. Geol. & Mijnb. 51: 641–643.

———. 1982. Paleoecology of tropical South America. *In:* G. T. Prance (ed.), Biological Diversification in the Tropics. Columbia University Press, New York. pp. 60–66.

———. 2001. Paleoecology of Amazonia. *In:* I. C. Guimarães Vieira, J. M. Cardoso da Silva, D. C. Oren, and M. A. D'Incao (organizers), Diversidad Biológica e Cultural da Amazônia. Museu Paraense Emílio Goeldi, Belém, Brazil.

——— and M. L. Absy. 1994. Amazonia during the last glacial. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 247–261.

——— and C. Garcia de Mutis. 1966. The Paleocene pollen flora of Colombia. Leidse Geol. Mededel. 35: 105–116.

——— and E. Gonzalez. 1960a. Upper Pleistocene and Holocene climate and vegetation of the "Sabana de Bogota" (Colombia, South America). Liedse Geol. Meded. 25: 261–315.

——— and ———. 1960b. Holocene and late-glacial climate and vegetation of Páramo de Palacio. Geol. & Mijnb. 22: 737–746.

——— and H. Hooghiemstra. 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. Quatern. Sci. Rev. 19: 725–742.

Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. *In:* J. L. Betancourt, T. R. Van Devender, and P. S. Martin (eds.), Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson. pp. 104–133.

Vanzolini, P. E. 1973. Paleoclimates, relief, and species multiplication in equatorial forests. *In:* B. Meggers, E. S. Ayensu, and W. D. Duckworth (eds.), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Institution Press, Washington, D.C. pp. 255–258.

——— and E. E. Williams. 1970. South American anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. São Paulo 19: 1–240.

Veblen, T. T., R. S. Hill, and J. Read (eds.). 1996. The Ecology and Biogeography of *Nothofagus* Forest. Yale University Press, New Haven, CT.

Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771–780.

Wallace, A. R. 1849. On the monkeys of the Amazon. Proc. Zool. Soc. London 20: 107–110.

———. 1876. The Geographical Distribution of Animals. Hafner, New York.

Walter, H. S. 2004. Understanding places and organisms in a changing world. Taxon 53: 905–910.

Webb, R. S., D. H. Rind, S. J. Lehman, R. J. Healy, and D. Sigman. 1997. Influence of ocean heat transport on the climate of the Last Glacial Maximum. Nature 385: 695–699.

Webb, S. D. 1991. Ecogeography and the great American interchange. Paleobiology 17: 266–280.

———. 1997. The great American faunal interchange. *In:* A. G. Coates (ed.), Central America: A Natural and Cultural History. Yale University Press, New Haven, CT. pp. 97–122.

———. 2006. The great American biotic interchange: Patterns and processes. *In:* A. Graham (ed.), The Biogeography of Latin America—Causes and Effects. Ann. Missouri Bot. Gard. 93: 245–257.

——— and A. Rancy. 1996. Late Cenozoic evolution of the Neotropical mammal fauna. *In:* J. B. C. Jackson, A. F. Budd, and A. G. Coates (eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago. pp. 335–358.

Webster, P. J., G. J. Holland, J. A. Curry, and H.-R. Chang. 2005. Changes in tropical cyclone number, direction, and intensity in a warming environment. Science 309: 1844–1846.

Wehr, W. C. and C. R. Manchester. 1996. Paleobotanical significance of Eocene flowers, fruits, and seeds from Republic, Washington. Wash. Geol. 24: 25–27.

Westgate, J. W. and C. T. Gee. 1990. Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 78: 163–177.

Whitmore, T. C. and G. T. Prance. 1987. Biogeography and Quaternary History in Tropical America. Oxford Monographs on Biogeography No. 3. Oxford Science Publications, Oxford, U.K.

Wijninga, V. M. 1996. Paleobotany and Palynology of Neogene Sediments from the High Plain of Bogotá (Colombia). Evolution of the Andean flora from the Paleoecological Perspective. Ph.D. Dissertation, University of Amsterdam, Amsterdam. (Reprinted in *The Quaternary of Colombia*, Vol. 21.)

Wiley, E. O. 1988. Vicariance biogeography. Ann. Rev. Ecol. Syst. 19: 513–542.

Winkworth, R. and L. Lohmann (organizers). 2005. The impact of plant dispersal on biogeography: Current understanding and prospects. Symposium, XVII International Botanical Congress, Vienna.

Wolfe, J. A. 1975. Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. Ann. Missouri Bot. Gard. 62: 264–279.

Wrenn, J. H., J.-P. Suc, and S. A. G. Leroy (eds.). 1999. The Pliocene: Time of Change. American Association of Stratigraphic Palynologists Foundation, Dallas.

Wright, S., J. Keeling, and L. Gillman. 2006. The road from Santa Rosalia: A faster tempo of evolution in tropical climates. Proc. Natl. Acad. Sci. U.S.A. 103: 7718–7722.

Wüster, W. et al. (+ 5 authors). 2005a. Tracing an invasion: Landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). Molec. Ecol. 14: 1095–1108.

——— et al. (+ 5 authors). 2005b. No rattlesnakes in the rainforests: Reply to Gosling and Bush. Molec. Ecol. 14: 3619–3621.

Wyss, A. R. et al. (+ 6 authors). 1993. South America's earliest rodent and recognition of a new interval of mammalian evolution. Nature 365: 434–437.

Zachos, J. C. et al. (+ 11 authors). 2005. Rapid acidification of the ocean during the Paleocene–Eocene thermal maximum. Science 308: 1611–1615.

Zamaloa, M. del C. 1992. A new species of *Nothofagidites*, *N. americanus*, from Patagonia and Antarctica. Rev. Palaeobot. Palynol. 72: 49–53.

——— and V. D. Barreda. 1992. *Nothofagidites tehuelchesii*, a new species from the Tertiary of Patagonia. Rev. Palaeobot. Palynol. 72: 55–59.

Zavada, M. S. and S. E. de Villiers. 2000. Pollen of the Asteraceae from the Paleocene–Eocene of South Africa. Grana 39: 39–45.

Ziegler, A. M. et al. (+ 5 authors). 2003. Tracing the tropics across land and sea: Permian to present. Lethaia 36: 227–254.

ADDITIONAL REFERENCES/GENERAL READINGS/ ELECTRONIC ADDRESSES

Chakrabarty, P. 2006. Systematics and historical biogeography of Greater Antillean Cichlidae. Molec. Phylogen. Evol. 39: 619–627.

Cifelli, R. L. and C. L. Gordon. 2007. Re-crowning mammals. Nature 447: 918–920.

Colinvaux, P. 2007. Amazon Expeditions: My Quest for the Ice-Age Equator. Yale University Press, New Haven, CT.

Collinson, M. E., M. C. Boulter, and P. L. Holmes. 1993. Magnoliophyta ("Angiospermae"). *In:* M. J. Benton (ed.), The Fossil Record 2. Chapman & Hall, London.

Cowling, S. A. 2004. Tropical forest structure: A missing dimension to Pleistocene landscapes. J. Quatern. Sci. 19: 733–743.

Crepet, W. L. and M. A. Gandolfo (organizers). 2008. Paleobotany in the Post-genomics Era. Ann. Missouri Bot. Gard. 95: 1–198.

Crisci, J. V. 2006. One-dimensional systematist: Perils in a time of steady progress. Syst. Bot. 31: 217–221.

Deep Time Project. Deep Time Project: A Comprehensive Phylogenetic Tree of Living and Fossil Angiosperms. http://www.flmnh.ufl.edu/deeptime/datingdivergences.html. [Dating divergences, molecular data.]

Donaghue, P. C. J. and M. J. Benton. 2007. Rocks and clocks: Calibrating the Tree of Life using fossils and molecules. Trends Ecol. Evol. 22: 424–431.

Doyle, J. A., H. Sauquet, T. Scharaschkin, and A. Le Thomas. 2004. Phylogeny, molecular and fossil dating, and biogeographic history of Annonaceae and Myristicaceae (Magnoliales). Int. J. Pl. Sci. 165(Suppl.): S55–S67.

Emanuel, K. 2005. Divine Wind: The History and Science of Hurricanes. Oxford University Press, Oxford, U.K. [See review by H. B. Bluestein, Nature 437: 953–954.]

Funk, V. A., A. Susanna, T. Stuessy, and R. Bayer (eds.). 2009. Systematics, Evolution, and Biogeography of Compositae. International Association for Plant Taxonomy, Vienna.

Haberle, S. G. 1997. Upper Quaternary vegetation and climate history of the Amazon Basin: Correlating marine and terrestrial pollen record. Proc. Ocean Drilling Program,

Scientific Results, Amazon Fan, 155: 381–396.
——— and M. A. Maslin. 1999. Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site. Quatern. Res. 51: 27–38.
Hedges, S. B. and S. Kumar. 2004. Precision of molecular time estimates. Trends Genet. 20: 242–247.
Hooghiemstra, H. 1999. Neotropical rain forest refugia during the last ice-age: Bridging the gap between concepts and data. Abstract, VII Congresso da ABEQUA, Porto Seguro, Bahia, Brazil (3–9 October 1999). 3 pp.
Huntingford, C. and J. Gash. 2005. Editorial: Climate equity for all. Science 309: 1789.
Irion, G. et al. (+ 8 authors). 2006. A multiproxy palaeoecological record of Holocene lake sediments from the Rio Tapajós, eastern Amazonia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 240: 523–535.
Kerr, R. A. 2005. Is Katrina a harbinger of still more powerful hurricanes? Science 309: 1807.
———. 2006. Global warming may be homing in on Atlantic hurricanes. Science 314: 910–911.
Krassilov, V. and N. Silantieva. 2005. Plant evolution in the Late Cretaceous (Turonian) of the southern Negev, Israel. Israel J. Pl. Sci. 53: 55–64. [Reports plants of combretaceous and rhizophoraceous affinity from the upper part of the Ora Formation.]
Lewin, R. 1988. The stamp of history and ecology in Amazonia. Science 240: 1619.
Magallón-Puebla, S. A. 2004. Dating lineages: Molecular and paleontological approaches to the temporal framework of clades. Int. J. Pl. Sci. 165(Suppl.): S7–S21.
Mayle, F. E. 2004. Assessment of the Neotropical dry forest refugia hypothesis in the light of palaeoecological data and vegetation model simulations. J. Quatern. Sci. 19: 713–720.
McDade, L. A., T. F. Daniel, C. A. Kiel, and K. Vollesen. 2005. Phylogenetic relationships among Acantheae (Acanthaceae): Major lineages present contrasting patterns of molecular evolution and morphological differentiation. Syst. Bot. 30: 834–862.
Moles, A. T. et al. (+ 5 authors). 2005. A brief history of seed size. Science 307: 576–580.
Mooney, C. 2007. Storm World: Hurricanes, Politics, and the Battle over Global Warming. Harcourt, New York. [See review by Elsner, Nature 448 (2007): 648.]
Morley, R. J. 2003. Interplate dispersal paths for megathermal angiosperms. Perspect. Pl. Ecol. Evol. Syst. 6: 5–20.
Nagashimam, K. et al. (+ 5 authors). 2007. Orbital- and millennial-scale variations in Asian dust transport path to the Japan Sea. Palaeogeogr. Palaeoclimatol. Palaeoecol. 247: 144–161.
Nyberg, J. et al. (+ 5 authors). 2007. Low Atlantic hurricane activity in the 1970s and 1980s compared to the past 270 years. Nature 447: 698–701.
Pennington, R. T., Q. C. B. Cronk, and J. A. Richardson (eds.). 2004. Plant Phylogeny and the Origin of Major Biomes. Philos. Trans., Ser. B 359: 1453–1656.
Ramírez, S. R., B. Gravendeel, R. B. Singer, C. R. Marshall, and N. E. Pierce. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. Nature 448: 1042–1045.
Renner, S. S. 2004. Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. *In:* R. T. Pennington, Q. C. B. Cronk, and J. A. Richardson (eds), Plant Phylogeny and the Origin of Major Biomes. Philos. Trans., Ser. B 359: 1485–1494.
Skvarla, J. J., M. L. DeVore, and W. F. Chissoe. 2005. Lophate sculpturing of Vernonieae (Compositae) pollen. Rev. Palaeobot. Palynol. 133: 51–68.
Stace, C. A. 2005. Plant taxonomy and biosystematics—Does DNA provide all the answers? Taxon 54: 999–1007.
Teeling, E. C. et al. (+ 5 authors). 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307: 580–584. [Discusses origin of bats in Laurasia 52–50 Ma, subsequent diversification to constitute ~20% of present mammalian species, and the need for coordinated molecular paleontological studies in a group where an estimated 61% of the fossil record of bats may be missing.]
Time Magazine. 2005. Are we making hurricanes worse? The impact of global warming, the cost of coastal development, plus: Charting the Gulf Coast destruction. October 3, 2005.
Trenberth, K. 2005. Uncertainty in hurricanes and global warming. Science 308: 1753–1754.
Urrego, D. H., M. R. Silman, and M. B. Bush. 2005. The Last Glacial Maximum: Stability and change in a western Amazonian cloud forest. J. Quatern. Sci. 20: 693–701.
Weeks, A., D. C. Daly, and B. B. Simpson. 2005. The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. Molec. Phylogen. Evol. 35: 85–101.
Whitfield, J. 2007. Fossils challenge DNA in the dating game. Nature 447: 894–895.
Witze, A. 2006. Tempers flare at hurricane meeting. Nature 441: 11.

APPENDICES

APPENDIX 1

Modern plant formations and representative species. See References in Chapter 3 for bibliographic citations in Appendix 1. Spellings of names not in TROPICOS are according to the original author.

APPENDIX 1.1

Dominant and associated species in the plant formations of Veracruz, Mexico. Names in parentheses are vegetation types according to Gómez-Pompa (1973).

Desert

(*Nolina–Hectia–Agave* desert)

Dominants: *Agave obscura*, *Hechtia roseana*, *Nolina parviflora.*

Associated species: *Adolphia infesta*, *Aneilema karwinskiana*, *Aristida barbata*, *A. glauca*, *Bouvardia scabrida*, *Chrysactinia mexicana*, *Dalea melantha*, *Dasylirion acrotrichum*, *Dyssodia setifolia*, *Loeselia glandulosa*, *Lycurus phleoides*, *Mammillaria dealbata*, *M. elegans*, *Salvia canescens*, *S. coulteri*, *S. thymoides*, *Stipa tenuissima*, *Tradescantia brachyphylla.*

Shrubland/Chaparral–Woodland–Savanna

(Low thorn selva)

Abutilon triquetrum, *Acacia constricta*, *A. texensis*, *Achatocarpus nigricans*, *Boerhaavia erecta*, *Cordia alba*, *C. boissieri*, *Coursetia axillaris*, *Chlorophora tinctoria*, *Citharexylum berlandieri*, *Croton nitens*, *Erythroxylon areolatum*, *Eugenia liebmannii*, *Guazuma ulmifolia*, *Jacquinia axillaris*, *Malpighia punicifolia*, *Mimosa pigra*, *Morisonia americana*, *Nopalea cochenillifera*, *Parkinsonia aculeata*, *Phyllanthus micrandrus*, *Pithecellobium* sp., *Plumbago* sp., *Randia* sp., *Schoepfia schreberi*, *Solanum lanceifolium*, *Trichilia parvifolia*, *Zizyphus sonorensis.*

(Thorn scrub)

Gymnosperm: *Juniperus* aff. *flaccida.* Angiosperms: *Agave* sp., *Asclepias linaria*, *Bouvardia longiflora*, *Buddlei(j)a* aff. *skutchii*, *Bursera simaruba*, *Capparis incana*, *Capraria biflora*, *Condalia mirandana*, *Croton ciliatoglandulosus*, *Echinocactus* sp., *Esenbeckia berlandieri*, *Eupatorium espinosarum*, *Karwinskia humboldtiana*, *Mammillaria camptotricha*, *Myrtillocactus geometrizans*, *Nopalea* sp., *Notholaena sinuata*, *Opuntia* sp., *Pithecellobium flexicaule*, *Prosopis juliflora*, *Quercus eduardi*, *Randia* sp., *Yucca treculeana*, *Zanthoxylum fagara.*

(Savanna)

Andropogon altus, *A. bicornis*, *Bulbostylis* aff. *paradoxa*, *Byrsonima crassifolia*, *Cassia diphylla*, *Chamaesyce hyssopifolia*, *Coccocypselum* sp., *Cologania* sp., *Conostegia speciosa*, *Crotalaria sagittalis*, *Curatella americana*, *Dichromena ciliata*, *Diodia rigida*, *Eleocharis interstincta*, *Fuirena* sp., *Hibiscus costatus*, *Hyptis conferta*, *H.* aff. *rugosa*, *Kyllinga brevifolia*, *Melochia hirsuta*, *Mimosa pudica*, *Myrica cerifera*, *Olyra latifolia*, *Paurotis wrightii*, *Polygala* aff. *adenophora*, *Polygala* sp., *Psidium guajava*, *P. molle*, *Rhynchanthera mexicana*, *Rhynchospora* aff. *barbata*, R. aff. *longispicata*, *Russelia floribunda*, *Sauvagesia erecta*, *Setaria geniculata*, *Spermacoce haenkeana*, *Xyris ambigua*, *Zexmenia aurea.*

Grassland

(Saline grassland)

Actinella chrysanthemoides, *Alternanthera repens*, *Andropogon glomeratus*, *Aphanostephus humilis*, *Astragalus wootoni*, *Atriplex pueblensis*, *Batis maritima*, *Borrichia frutescens*, *Bouteloua breviseta*, *Croton dioicus*, *Cuscuta salina*, *Dichondra argentea*, *Distichlis spicata*, *Erodium cicutarium*, *Fimbristylis castanea*, *F. spathacea*, *Gomphrena dispersa*, *Heliotropium curassavicum*, *Houstonia rubra*, *Plantago nivea*, *Salicornia perennis*, *Sanvitalia procumbens*, *Scleropogon brevifolius*, *Spartina alterniflora*, *S. spartinae*, *Stipa editorum*, *Verbena canescens*, *V. ciliata.*

(Temperate grassland)

Ferns and allied groups: *Ophioglossum* sp., *Selaginella* sp. Angiosperms: *Anthericum* aff. *leucocomum*, *A. nanum*, *Asclepias glaucescens*, *A. rosea*, *Bulbostylis capillaris*, *Cologania procumbens*, *Commelina diffusa*, *Cyperus seslerioides*, *Eryngium carlinae*, *Heliotrophium fruticosum*, *Ipomoea muricata*, *Microchloa kunthii*, *Nemastylis tenuis*, *Oxalis* sp., *Quercus peduncularis*, *Ranunculus hookeri*, *Setaria geniculata*, *Sisyrinchium* sp., *Stevia elatior*, *Tridax procumbens*, *Verbena teucriifolia.*

Mangrove

(Mangrove forest)

Dominants: *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, *Rhizophora mangle.*

Associated species (some in only slightly saline water)—Fern: *Acrostichum aureum.* Angiosperms: *Amerimnon brownei*, *Annona glabra*, *Clerodendrum ligustrinum*, *Dalbergia ecastaphyllum*, *Diospyros digyna*, *Ficus insipida*, *Hibiscus tiliaceus*, *Piper nitidum*, *Pithecellobium disciferum*, *P. erythrocarpum*, *Randia aculeata*, *Rhabdadenia biflora*, *Sapium nitidum.*

Beach/Strand/Dune

(Coastal dune vegetation)

Gymnosperm: *Zamia furfuracea.* Angiosperms: *Acacia sphaerocephala*, *Agave* sp., *Allamanda cathartica*, *Amaranthus greggii*, *Ambrosia cumanensis*, *Andropogon glomeratus*, *A. littoralis*, *Antigonon leptopus*, *Batis maritima*, *Bidens squarrosa*, *Caesalpinia bonduc*, *Cakile lanceolata*, *Canavalia maritima*, *Casearia nitida*, *Cassia cinerea*, *Chamaesyce buxifolia*, *Chrysobalanus icaco*, *Citharexylum ellipticum*, *Cnidoscolus herbaceus*, *Coccoloba uvifera*, *Commelina erecta*, *Crossopetalum latifolium*, *Crotalaria* sp., *Croton punctatus*, *Cyperus ligularis*, *Eragrostis domingensis*, *Euphorbia buxifolia*, *Fimbristylis spathacea*, *Hymenocallis* sp., *Ipomoea pes-caprae*, *I. stolonifera*, *Iresine celosioides*, *Iva asperifolia*, *Jacquinia aurantiaca*, *J. pungens*, *Laguncularia racemosa*, *Merremia discoidesperma*, *Nectandra coriacea*, *Oenothera drummondii*, *Okenia hypogaea*, *Opuntia dillenii*, *Othake lindenii*, *Palafoxia texana*, *Panicum repens*, *Paspalum vaginatum*, *Phyla nodiflora*, *Pouteria durlandii*, *Psychotria nutans*, *Randia aculeata*, *R. laetevirens*, *Scaevola plumieri*, *Sesuvium portulacastrum*, *Sporobolus virginicus*, *Spartina patens*, *Stemodia tomentosa*, *Terminalia catappa*, *Tournefortia gnaphalodes*, *Uniola paniculata*, *Verbesina olivacea.*

Freshwater Herbaceous Bog/Marsh/Swamp

(Swamp or aquatic vegetation)

Bactris cohune, *Cyperus giganteus*, *Eleocharis interstincta*, *Pontederia sagittata*, *Thalia geniculata*, *Typha* sp.

Lowland Neotropical Rain Forest

(Tall evergreen selva)

Dominants: *Bernoullia flammea*, *Brosimum alicastrum*, *Calophyllum brasiliense*, *Dialium guianense*, *Ficus tecolutensis*, *Poulsenia armata*, *Pseudolmedia oxyphyllaria*, *Terminalia amazonia.*

Associated species—Ferns: *Lygodium*, *Sphaeropteris myosuroides.* Gymnosperm: *Podocarpus guatemalensis.* Angiosperms: *Albizzia purpusii*, *Alchornea latifolia*, *Andira galeottiana*, *A. inermis*, *Annona muricata*, *A. reticulata*, *Astrocaryum mexicanum*, *Astronium graveolens*, *Bactris baculifera*, *B. cohune*, *Brosimum alicastrum*, *Bursera simaruba*, *Castilla elastica*, *Ceiba pentandra*, *Cephaelis tomentosa*, *Chamaedorea alternans*, *C. ernesti-augusti*, *C. lindeniana*, *C. oblongata*, *C. tepejilote*, *Crat(a)eva tapia*, *Cupania dentata*, *Cymbopetalum baillonii*, *C. penduliflorum*, *Cynometra retusa*, *Dendropanax arboreus*, *Dussia mexicana*, *Ficus insipida*, *Genipa americana*, *Guarea bijuga*, *G. chichon*, *G. glabra*, *G. tonduzii*, *Guatteria amplifolia*, *Hampea nutricia*, *Hirtella racemosa*, *Jacaratia dolichaula*, *Licania hypoleuca*, *Licaria peckii*, *Lonchocarpus cruentus*, *L. guatemalensis*, *L. santarosanus*, *Malmea depressa*, *Matayba oppositifolia*, *Miconia argentea*, *Mortoniodendron guatemalense*, *Ormosia isthmensis*, *Picramnia antidesma*, *P. tetramera*, *Pimenta dioica*, *Pithecellobium arboreum*, *Pleuranthodendron mexicanum*, *Posoqueria latifolia*, *Poulsenia armata*, *Pouteria campechiana*, *Pseudolmedia oxyphyllaria*, *Psychotria* sp., *Pterocarpus hayesii*, *Quararibea funebris*, *Reinhardtia gracilor*, *Rheedia edulis*, *Rinorea guatemalensis*, *Robinsonella mirandae*, *Salacia belizensis*, *Sapium nitidum*, *Sapranthus* aff. *humilis*, *Scheelea liebmannii*, *Simarouba glauca*, *Sloanea tuerckheimii*, *Stemmadenia donnell-smithii*, *Sterculia apetala*, *S. mexicana*, *Swietenia macrophylla*, *Tabebuia rosea*, *Tapirira macrophylla*, *Tetrorchidium rotundatum*, *Thouinia paucidentata*, *Trichilia breviflora*, *T. hirta*, *T. tomentosa*, *Trophis mexicana*, *Turpinia* aff. *paniculata*, *Vatairea lundellii*, *Vochysia hondurensis*, *Xylopia frutescens*, *Zanthoxylum belizense*, *Zuelania guidonia.*

Palm stands (probably anthropogenic): Dominant—*Scheelea liebmannii*; Associated species—*Albizia purpusii*, *Bunchosia lanceolata*, *Citharexylum hexangulare*, *Cupania dentata*, *Pleuranthodendron mexicanum*, *Sapindus saponaria*, *Stemmadenia galeottiana*, *Trophis racemosa.*

Lower to Upper Montane Broad-Leaved Forest

(Low evergreen selva)

Ferns and allied genera: *Pteris* (tropical moist forest).

Angiosperms: *Clusia salvinii*, *Elleanthus capitalus*, *Gaultheria nitida*, *Ilex* sp., *Litsea* sp., *Monnina* sp., *Myrica cerifera*, *Oreopanax xalapense*, *Palicourea galeottiana*, *Rapanea juergensenii*, *Saurauia villosa*, *Senecio arborescens*, *Viburnum montanum.*

(Tall semi-evergreen selva)

Dominant: *Brosimum alicastrum.*

Associated species—Fern: *Sphaeropteris horrida.* Gymnosperm: *Ceratozamia mexicana.* Angiosperms: *Achras zapota*, *Alchornea latifolia*, *Ampelocera hottlei*, *Aspidosperma megalocarpon*, *Astronium graveolens*, *Beilschmiedia anay*, *B. mexicana*, *Bernoullia flammea*, *Bombax ellipticum*, *Bumelia persimilis*, *Bunchosia lanceolata*, *Bursera simaruba*, *Calatola laevigata*, *Capparis baducca*, *Carpodiptera ameliae*, *Castilla elastica*, *Cedrela odorata*, *Ceiba pentandra*, *Chamaedorea lunata*, *Chlorophora tinctoria*, *Cordia alliodora*, *Cupania dentata*, *Dalea elata*, *Dendropanax arboreus*, *Dioscorea mexicana*, *Diospyros digyna*, *Dussia mexicana*, *Enallagma latifolia*, *Exostema mexicanum*, *Exothea copalillo*, *Ficus cookii*, *F. insipida*, *F. lapathifolia*, *F. tecolutensis*, *Guazuma ulmifolia*, *Guettarda elliptica*, *Hampea integerrima*, *Hernandia sonora*, *Ilex spuria*, *Licaria peckii*, *Mastichodendron capiri*, *Miconia trinervia*, *Mirandaceltis monoica*, *Misanteca capitata*, *Myriocarpa bifurca*, *Myroxylon balsamum*, *Nectandra salicifolia*, *N. sanguinea*, *Nephelea mexicana*, *Ocotea veraguensis*, *Perrottetia longistylis*, *Persea schiedeana*, *Phoebe mexicana*, *Pilea pubescens*, *Pimenta dioica*, *Piper sanctum*, *Pithecellobium arboreum*, *Platymiscium yucatanum*, *Pleuranthodendron mexicanum*, *Poulsenia armata*, *Protium copal*, *Quercus corrugata*, *Q.* aff. *gracilis*, *Q. skinneri*, *Robinsonella mirandae*, *Sapindus saponaria*, *Sapium lateriflorum*, *Saurauia laevigata*, *Scheelea liebmannii*, *Sickingia rhodoclada*, *Stemmadenia donnell-smithii*, *Swietenia macrophylla*, *Tapiria mexicana*, *Trichilia havanensis*, *T. hirta*, *Trimeza martinicensis*, *Trophis racemosa*, *Ulmus mexicana*, *Urera baccifera*, *U. caracasana*, *Vatairea lundellii*, *Virola guatemalensis*, *Zuelania guidonia.*

(Medium semi-evergreen selva)

Transitional vegetation between the drier phases of the tall selva and the mesic phases of the low selva (15–25 m tall, ~40% deciduous, drier areas with 1400 mm or more rainfall but with a pronounced dry season).

(Low semi-evergreen selva)

Acrocomia mexicana, *Byrsonima crassifolia*, *Coccoloba barbadensis*, *Crescentia cujete*, *Curatella americana*, *Psidium guajava*.

(Low deciduous selva)

Dominants: *Cordia dodecandra*, *Crescentia alata*, *Enterolobium cyclocarpum*, *Piscidia piscipula*, *Tabebuia chrysantha*, *T. rosea*.

Associated species—Gymnosperm: *Dioon edule*. Angiosperms: *Acacia cornigera*, *A. farnesiana*, *Acanthocereus pentagonus*, *Aeschynomene compacta*, *Agave* sp., *Bromelia pinguin*, *Bunchosia biocellata*, *Bursera bipinnata*, *B. fagaroides*, *B. simaruba*, *Byrsonima crassifolia*, *Casearia nitida*, *Celtis iguanaea*, *Chlorophora tinctoria*, *Citharexylum ellipticum*, *Comocladia engleriana*, *Cordia pringlei*, *Coutarea hexandra*, *Crataeva tapia*, *Croton glandulosepalus*, *C. punctatus*, *Cupania macrophylla*, *Curatella americana*, *Dalbergia glabra*, *Daphnopsis brevifolia*, *Erythroxylum areolatum*, *Eugenia liebmannii*, *Ficus cotinifolia*, *F. maxima*, *F. obtusifolia*, *Guettarda elliptica*, *Haematoxylum brasiletto*, *Hamelia patens*, *Jatropha pseudocurcas*, *Luehea speciosa*, *Maba verae-crucis*, *Nopalea dejecta*, *Okenia hypogaea*, *Opuntia puberula*, *Parmentiera edulis*, *Phyllanthus grandifolius*, *P. nobilis*, *Pithecellobium calostachys*, *P. erythrocarpum*, *Plumeria acutifolia*, *Randia aculeata*, *R. albonervia*, *Sabal mexicana*, *Sageretia elegans*, *Salvia coccinea*, *Sapium* sp., *Tamonea curassavica*, *Thouinidium decandrum*, *Trichilia havanensis*, *T. parvifolia*, *Zanthoxylum fagara*, *Zuelania guidonia*.

(Deciduous forest association)

Dominants: *Engelhardia mexicana*, *Liquidambar macrophylla*, *Meliosma alba*, *Quercus affinis*, *Q. skinneri*, *Ulmus mexicana*.

Associated species—Ferns and allied groups: *Cyathea fulva*, *Lycopodium cernuum*. Gymnosperm: *Podocarpus matudae*. Angiosperms: *Alfaroa mexicana*, *Ardisia hyalina*, *Befaria glauca*, *Brunellia mexicana*, *Calyptranthes karwinskyana*, *Carpinus caroliniana*, *Centradenia salicifolia*, *Cestrum endlicheri*, *C. fasciculatum*, *Clethra quercifolia*, *C. serrulata*, *Coccocypselum hirsutum*, *Conostegia arborea*, *Cornus florida*, *Deppea grandiflora*, *D. purpusii*, *Diospyros riojae*, *Dussia mexicana*, *Eugenia trunciflora*, *Fagus mexicana*, *Guarea chichon*, *Heliconia bihai*, *H. schiedeana*, *Hoffmannia orizabensis*, *Ilex vomitoria*, *Inga latibracteata*, *Juglans pyriformis*, *Klugia azurea*, *Loasa triphylla*, *Magnolia schiedeana*, *Marsdenia macrophylla*, *Meliosma alba*, *Nephelea mexicana*, *Olmediella betschleriana*, *Oreopanax liebmannii*, *Ostrya virginiana*, *Palicourea galeottiana*, *Peperomia deppeana*, *P. glabella*, *P. obtusifolia*, *Perrottetia longistylis*, *Persea cinerascens*, *Phoebe acuminatissima*, *P. gentlei*, *Pithecellobium vulcanorum*, *Prunus brachybotrya*, *P. tetradenia*, *Psychotria* aff. *trichotoma*, *Quercus corrugata*, *Q. ocoteaefolia*, *Q. pilarius*, *Richardia scabra*, *Rondeletia bourgaei*, *R. capitellata*, *Salvia amarissima*, *Sambucus mexicana*, *Saurauia villosa*, *Senecio grandifolius*, *Sloanea* sp., *Solanum laurifolium*, *Styrax glabrescens*, *Talauma mexicana*, *Ternstroemia sylvatica*, *Tetranema mexicanum*, *Tillandsia polystachia*, *Tournefortia petiolaris*, *Trichilia glabra*, *Triumfetta dumetorum*, *Turpinia insignis*, *T.* aff. *paniculata*, *Verbena carolina*, *Viburnum tiliifolium*, *Xylosma flexuosa*, *X. quichensis*, *Weinmannia pinnata*, *Zanthoxylum kellermanii*.

Broad-leaved (oak) forest: Dominant—*Quercus oleoides*. Associated species—Fern: *Pteridium aquilinum*. Angiosperms: *Alchornea latifolia*, *Byrsonima crassifolia*, *Coccoloba barbadensis*, *Conostegia xalapensis*, *Curatella americana*, *Dendropanax arboreus*, *Ficus maxima*, *Genipa caruto*, *Sapium lateriflorum*, *Tapirira macrophylla*, *Waltheria brevipes*, *Xylosma flexuosa*, *Zinowiewia integerrima*, *Zuelania guidonia*.

Coniferous Forest

(Needle-leaved and scale-leaved forest)

Dominants—Gymnosperms: *Pinus hartwegii*, *P. oocarpa*, *P. pseudostrobus*, *P. teocote*, *P. rudis*, *P. strobus* var. *chiapensis*.

Associated species—Ferns: *Cheilanthes microphylla*, *Cyathea costaricensis*, *Lophosoria quadripinnata*, *Pteridium aquilinum*. Gymnosperms: *Abies religiosa*, *Pinus ayacahuite*, *P. leiophylla*, *P. montezumae*, *P. patula*, *Zamia loddigesii*. Angiosperms: *Agave xalapensis*, *Alchemilla pectinata*, *A. vulcanica*, *Alibertia edulis*, *Alnus arguta*, *Arbutus glandulosa*, *Arenaria bryoides*, *A. lycopodioides*, *A. serpens*, *Arundinella deppeana*, *Ascyrum hypericoides*, *Baccharis conferta*, *Bidens triplinervia*, *Brosimum alicastrum*, *Brunellia mexicana*, *B. vulgaris*, *Bulbostylis papillosa*, *Byrsonima crassifolia*, *Calea integrifolia*, *C. manicata*, *C. urticifolia*, *Castilleja longibracteata*, *Cerastium orithales*, *C. vulcanicum*, *Chimaphila maculata*, *Clethra macrophylla*, *Cnicus jorullensis*, *Cornus disciflora*, *C. excelsa*, *Croton nitens*, *C. repens*, *Crusea calocephala*, *Diphysa floribunda*, *Eryngium proteaeflorum*, *Erythraea macrantha*, *Eupatorium aschenbornianum*, *E. morifolium*, *Galium uncinulatum*, *Gnaphalium brachypterum*, *Halenia brevicornis*, *H. nudicaulis*, *H. paucifolia*, *Hampea integerrima*, *Lagascea helianthifolia*, *Lantana hispida*, *Leucothoe mexicana*, *Lippia hypoleia*, *Liquidambar macrophylla*, *Litsea glaucescens*, *Lupinus elegans*, *L. montanus*, *L. vaginatus*, *Lythrum acinifolium*, *Malaxis soulei*, *Monochaetum floribundum*, *Mosquitoxylum jamaicense*, *Myrica cerifera*, *Nephelea mexicana*, *Oxalis decaphylla*, *Oxylobus arbutifolius*, *Parathesis serrulata*, *Paspalum pectinatum*, *P. plicatulum*, *Penstemon gentianoides*, *Pinguicula caudata*, *Potentilla richardii*, *Quercus candicans*, *Q. castanae*, *Q. crassifolia*, *Q. excelsa*, *Q. mexicana*, *Q. xalapensis*, *Ranunculus dichotomus*, *Rapanea myricoides*, *Relbunium hypocarpium*, *Rubus adenotrichu(o)s*, *Rumex acetosella*, *Saurauia pedunculata*, *S. serrata*, *Sauvagesia erecta*, *Senecio grandifolius*, *S. schaffneri*, *Solanum torvum*, *Spilanthes americana*, *Ternstroemia sylvatica*, *Stenanthium frigidum*, *Stipa ichu*, *Vernonia deppeana*.

Alpine Tundra (Páramo)

Fern: *Asplenium castaneum*. Angiosperms: *Cnicus nivalis*, *Draba jorullensis*, *D. myosotidioides*, *Festuca* sp., *Gnaphalium inornatum*, *G. oxyphyllum*, *G. popocatepecuana*, *Muhlenbergia* sp., *Senecio chrysactis*, *S. galeottii*, *S. orizabensis*, *Stipa* sp.

APPENDIX 1.2

Prominent species of the plant formations of Chiapas, Mexico (Breedlove, 1973, 1981, first name in parentheses; see also Graham, 1999, pp. 25–29). Additional names in parentheses are those used by other authors for all or part of the same formation.

Shrubland/Chaparral–Woodland–Savanna

(Short-tree savanna; sabana, selva baja subperennifolia, vegetación sabanoide)

Common trees: *Byrsonima crassifolia*, *Crescentia alata*, *C. cujete*, *Curatella americana*.

Other trees: *Acacia pennatula*, *Alvaradoa amorphoides*, *Cordia dodecandra*, *Palmae*, *Piscidia piscipula*, *Quercus oleoides*, *Tetracera volubilis*.

Thorn woodland; selva baja espinosa caducifolia, bosque espinoso, tropical and subtropical thorn woodland: *Acacia cochliacantha*, *A. cornigera*, *A. farnesiana*, *A. pringlei*, *Bauhinia pauletia*, *Buttneria aculeata*, *Bursera diversifolia*, *Casearia nitida*, *Cordia curassavica*, *C. spinescens*, *Croton guatemalensis*, *Diphysa floribunda*, *Erythroxylum havanense*, *Jacquinia aurantiaca*, *Karwinskia calderonii*, *Piptadenia flava*, *Pisonia macranthocarpa*, *Pithecellobium dulce*, *Randia aculeata*, *Sageretia elegans*, *Stenocereus* sp.

Grassland

Bunch grassland; zacatonal: *Briza rotundata*, *Bromus carinatus*, *Festuca amplissima*, *Muhlenbergia gigantea*, *M. macroura*, *M. robusta*, *Stipa ichu*, *S. virescens*, *Trisetum irazuense*.

Mangrove Swamp

Avicennia germinans, *Batis maritima*, *Conocarpus erecta*, *Laguncularia racemosa*, *Philoxerus vermicularis*, *Rhizophora samoensis*.

Freshwater Herbaceous Bog/Marsh/Swamp

Herbaceous marsh; tulare, popal, includes aquatic: *Caladium jamaicense*, *Calathea* sp., *Caperonia palustris*, *Carex* sp., *Cyperus* sp., *Heliconia bihai*, *Hymenachne amplexicaulis*, *Juncus* sp., *Leersia* sp., *Ludwigia peruviana*, *Lythrum vulneraria*, *Neptunia plena*, *Nymphaea blanda*, *Paspalum* sp., *Phragmites australis*, *Rhynchospora* sp., *Scirpus californicus*, *Sesbania emerus*, *Thalia geniculata*, *Typha latifolia*.

Lowland Neotropical Rain Forest

(Tropical rain forest; selva alta perennifolia [tall evergreen selva], selva alta siempre, bosque tropical perennifolio)

Canopy trees: *Aspidosperma megalocarpon*, *Brosimum alicastrum*, *Dialium guianense*, *Erblichia xylocarpa*, *Ficus* sp., *Guatteria anomala*, *Manilkara achras*, *Poulsenia armata*, *Protium copal*, *Swietenia macrophylla*, *Talauma mexicana*, *Tapirira mexicana*, *Terminalia amazonia*, *Vatairea lundellii*.

Understory and lower trees of the canopy: *Alchornea latifolia*, *Alibertia edulis*, *Belotia campbellii*, *Blepharidium mexicanum*, *Bumelia persimilis*, *Bursera simaruba*, *Cassia grandis*, *Cephaelis tomentosa*, *Dracaena americana*, *Forchhammeria trifoliata*, *Guarea excelsa*, *Hasseltia dioica*, *Hirtella racemosa*, *Lacistema aggregatum*, *Licaria peckii*, *Orthion subsessile*, *Ouratea lucens*, *Wimmeria bartlettii*, *Zuelania guidonia*.

Palm forest: *Sabal mexicana*, *Scheelea liebmannii*, *S. preussii*.

Temperate riparian forest: *Acer negundo* var. *mexicanum*, *Alnus acuminata* ssp. *acuminata*, *Baccharis heterophylla*, *Berchemia scandans*, *Cornus excelsa*, *Crataegus pubescens*, *Cuphea hyssopifolia*, *Platanus chiapensis*, *Salix bonplandiana*, *S. taxifolia*.

Lower to Upper Montane Broad-Leaved Forest

(Lower montane rain forest; low evergreen selva, selva alta siempreverde, selva alta perennifolia, bosque tropical perennifolio, tropical premontane moist, wet, or rain forest)

Canopy trees (many as in the tropical rain forest): *Alseis yucatanensis*, *Belotia mexicana*, *Calophyllum brasiliense*, *Chaetoptelea* (*Ulmus*) *mexicana*, *Licania platypus*, *Nectandra sinuata*, *Ocotea rubriflora*, *Quercus oleoides*, *Q. skinneri*, *Sebastiania longicuspis*, *Talauma mexicana*, *Vochysia hondurensis*.

Understory and lower trees of the canopy: *Chrysophyllum mexicanum*, *Cleidion oblongifolium*, *Cymbopetalum penduliflorum*, *Faramea occidentalis*, *Piper* sp., *Pseudolmedia spuria*, *Rhacoma eucymosa*, *Rinorea guatemalensis*, *Sloanea terniflora*, *Stemmadenia donnell-smithii*, *Trophis racemosa*.

(Montane rain forest; selva mediana y baja siempreverde, selva mediana or baja perennifolia, bosque tropical perennifolio, tropical montane moist, wet, or rain forest)

Canopy trees: *Alfaroa mexicana*, *Ardisia alba*, *Brunellia mexicana*, *Hedyosmum mexicanum*, *Hyperbaena mexicana*, *Lunania mexicana*, *Matudaea trinervia*, *Meliosma matudai*, *Mirandaceltis monoica*, *Mosquitoxylum jamaicense*, *Nectandra reticulata*, *Oecopetalum mexicanum*, *Oreopanax sanderianus*, *O. xalapensis*, *Platanus chiapensis*, *Quercus oocarpa*, *Q. peduncularis*, *Synardisia venosa*, *Trichilia erythrocarpa*, *Turpinia occidentalis*.

Understory and lower trees/shrubs of the canopy: *Acalypha skutchii*, *Billia hippocastanum*, *Centropogon cordatus*, *Cephaelis axillaris*, *C. elata*, *Chamaedorea concolor*, *Eugenia ravenii*, *Hampea longipes*, *Miconia lauriformis*, *Mollinedia guatemalensis*, *Oreopanax liebmanii*, *Palicourea* sp., *Parathesis microcalyx*, *Psychotria* sp., *Siparuna nicaraguensis*, *Trophis mexicana*, *Urera alceifolia*.

(Evergreen cloud forest; cloud forest, selva mediana y baja siempreverde, selva mediana or baja perennifolia, subtropical montane wet or rain forest)

Canopy trees—Gymnosperms: *Abies guatemalensis*, *Pinus ayacahuite*, *Podocarpus matudae*. Angiosperms: *Acer negundo*, *Chiranthodendron pentadactylon*, *Clethra lanata*, *C. oleoides*, *Drimys*

granadensis, *Magnolia sharpii*, *Meliosma matudae*, *Microtropis contracta*, *Olmediella betschleriana*, *Oreopanax capitatus*, *Persea donnell-smithii*, *P. schiedeana*, *Photinia matudae*, *Quercus hondurensis*, *Weinmannia pinnata*, *Wimmeria chiapensis*, *Zinowiewia rubra*.

Understory shrubs: *Cavendishia crassifolia*, *Cleyera theoides*, *Deppea grandiflora*, *Eugenia tonii*, *Fuchsia microphylla* subsp. *aprica*, *F. paniculata*, *Gentlea micrantha*, *Greigia oaxacana*, *Mahonia paniculata*, *Miconia ravenii*, *Rapanea juergensenii*, *Saurauia oreophila*, *Symplocos breedlovei*, *Vaccinium confertum*.

(Evergreen seasonal forest; selva alta subdecidua, selva alta or mediana subperennifolia, selva alta or mediana subcaducifolia, bosque tropical perennifolio, tropical or subtropical or tropical premontane moist forest)

Trees: *Astronium graveolens*, *Bernoullia flammea*, *Brosimum alicastrum*, *Bumelia persimilis*, *Calycophyllum candidissimum*, *Ceiba pentandra*, *Coccoloba barbadensis*, *Cordia alliodora*, *Cupania dentata*, *Elaeodendron trichotomum*, *Enterolobium cyclocarpum*, *Ficus glaucescens*, *Guettarda combsii*, *Hymenaea courbaril*, *Lafoensia punicaefolia*, *Licania arborea*, *Platymiscium dimorphandrum*, *Rheedia edulis*, *Sapium macrocarpum*, *Sterculia mexicana*, *Styrax argenteus*, *Tabebuia chrysantha*, *Vatairea lundellii*.

Shrubs and small trees: *Amyris chiapensis*, *Ardisia escallonioides*, *Bourreria huanita*, *Calyptranthes chiapensis*, *Clusia flava*, *Eugenia acapulcensis*, *Gentlea venosissima*, *Karwinskia calderonii*, *Psychotria erythrocarpa*.

(Tropical deciduous forest; deciduous seasonal forest, selva baja decidua, selva baja caducifolia, bosque tropical deciduo, tropical or subtropical dry and very dry forest)

Annona sp., *Bucida macrostachya*, *Bursera excelsa*, *B. simaruba*, *Calycophyllum candidissimum*, *Cecropia peltata*, *Cedrela oaxacensis*, *Ceiba aesculifolia*, *Cochlospermum vitifolium*, *Cordia alliodora*, *Eysenhardtia adenostylis*, *Gliricidia sepium*, *Godmania aesculifolia*, *Hauya elegans*, *Heliocarpus donnell-smithii*, *Hura polyandra*, *Ipomoea murucoides*, *Leucaena* sp., *Luehea candida*, *Lysiloma auritum*, *Plumeria rubra*, *Pseudobombax ellipticum*, *Spondias mombin*, *Stemmadenia obovata*, *Swietenia humilis*, *Tabebuia chrysantha*, *T. rosea*, *Triplaris melaenodendron*.

Deciduous forest association (pine–oak–*Liquidambar* forest; cloud forest, deciduous forest, bosque deciduo, bosque caducifolio, bosque mesófilo de montaña, subtropical montane moist forest):

Trees—Gymnosperms: *Pinus chiapensis*, *P. montezumae*. Angiosperms: *Carpinus caroliniana*, *Cassia oxyphylla*, *Citharexylum donnell-smithii*, *Clethra suaveolens*, *Cornus disciflora*, *Cupania dentata*, *Erythrina chiapensis*, *Fraxinus uhdei*, *Liquidambar styraciflua*, *Meliosma dives*, *Montanoa hexagona*, *Nyssa sylvatica*, *Ostrya guatemalensis*, *Perrottetia ovata*, *Quercus candicans*, *Q. oocarpa*, *Q. polymorpha*, *Q. sapotifolia*, *Q. segoviensis*, *Q. skinneri*, *Rhus striata*, *Saurauia scabrida*, *Styrax glabrescens*, *Turpinia occidentalis*.

Understory shrubs: *Aphelandra gigantiflora*, *Baccharis trinervis*, *Bocconia gracilis*, *Cestrum guatemalensis* var. *gracile*, *Fuchsia microphylla* subsp. *quercetorum*, *Gaultheria odorata*, *Guamatela tuerckheimii*, *Hibiscus bifurcatus* var. *pilosus*, *Liabum glabrum* var. *hypoleucum*, *Parathesis chiapensis*, *Phenax mexicanus*, *Rapanea myricoides*, *Rhus terebinthifolia*, *Solanum brachystachys*, *Symplocos longipes*, *Triumfetta grandiflora*, *Verbesina perymenioides*, *Viburnum hartwegii*.

Swamp and lowland riparian forest; canacoital—Gymnosperm: *Taxodium mucronatum*. Angiosperms: *Andira galeottiana*, *Bravaisia integerrima*, *Bucida buceras*, *Calophyllum brasiliense* var. *rekoi*, *Haematoxylum campechianum*, *Pachira aquatica*, *Salix chilensis*.

Alpine Tundra (Páramo)

(Evergreen cloud scrub; páramo, páramos de altura, tropical or subtropical montane or subalpine moist, wet, or rain páramo)

Ferns and allied groups: *Gleichenia* sp., *Lycopodium* sp. Angiosperms: *Alchemilla pinnata*, *Arenaria bryoides*, *Beschorneria chiapensis*, *Calamagrostis tolucensis*, *Gaultheria cumingii*, *G. odorata*, *Gnaphalium vulcanicum*, *Haplopappus stoloniferus*, *Holodiscus argenteus*, *Lupinus montanus*, *Luzula racemosa*, *Muehlenbeckia volcanica*, *Myrrhidendron donnell-smithii*, *Pernettya ciliata*, *P. hirsuta*, *P. tomasii*, *Potentilla heterosepala*, *Ternstroemia tepezapote*, *Trisetum irazuense*, *Vaccinium confertum*, *V. haematinum*, *V. matudae*, *V. minarum*, *Weldenia candida*, *Werneria nubigena*.

Second-growth and successional forest, and shrub associations (phases): *Abutilon tridens*, *Acacia augustissima*, *Arctostaphylos lucida*, *Baccharis (pseudo)vaccinioides*, *Calliandra grandiflora*, *C. houstoniana*, *Ceanothus co(a)eruleus*, *Clibadium arboreum*, *Coaxana ebracteata*, *Lantana hirta*, *L. hispida*, *Lippia hypoleia*, *Malvaviscus arboreus*, *Muehlenbeckia tamnifolia*, *Pavonia paniculata*, *Rhamnus discolor*, *R. nelsonii*, *Rubus* sp., *Salvia* sp., *Smallanthus maculatus*, *Tithonia diversifolia*, *T. longiradiata*, *Vernonia leiocarpa*, *Viburnum lautum*.

APPENDIX 1.3

Summary of the principal extant genera mentioned in the text and appendices that characterize the plant formations of Mexico, with fossil representatives. An asterisk (*) indicates some of the genera reported from Late Cretaceous to Tertiary deposits of Mexico (Quaternary occurrences are listed in Table 4.1). A double asterisk (**) indicates the genus may be present, but the fossil(s) can only be referred to a broader taxonomic category (viz., a group of genera, family, or group of families). Taxa may range through more than one formation, and some may have changed associations from Cretaceous through ~middle Eocene times (see I: pp. 124, 332). In addition to the reports of megafossils in the older literature, some microfossil assemblages studied more recently include an unusually high number of unexpected identifications. All would benefit from confirmation and entry into a monitored database. Families fide original authors.

Desert

Gymnosperm: **Ephedra*. Angiosperms: **Acacia*, *Agave*, **Ambrosia* (widespread; late Pliocene), **Artemisia* (late Pliocene), *Beaucarnea*, **Bursera* (widespread), *Cercidium*, *Dalea*, *Dasylirion*, *Flourensia*, *Fouquieria*, *Idria*, *Jatropha*, *Koeberlinia*, *Larrea*, *Leucophyllum*, *Lysiloma*, **Mimosa*, *Olneya*, *Parkinsonia*, *Parthenium*, *Prosopis*, and *Yucca*, in addition to numerous Cactaceae, **chenoams, and **Gramineae.

Shrubland/Chaparral–Woodland–Savanna

**Acacia*, *Agave*, *Byrsonima*, **Bursera*, *Caesalpinia*, **Casearea*, **Cedrela*, *Ceiba*, **Celtis*, *Cercidium*, **Cercocarpus*, **Comocladia*, *Curatella*, *Cyrtocarpa*, **Daphnopsis*, *Euphorbia*, *Fouquieria*, *Haematoxylon*, **Hymenaea*, *Ipomoea*, *Jatropha*, **Karwinskia*, *Lippia*, *Lysiloma*, **Mimosa*, *Paurotis*, *Piscidia*, **Pistacia*, *Pithecellobium*, and *Prosopis*, together with some Cactaceae and numerous **chenoams and **Gramineae.

Grassland

Grasses range throughout most of the plant formations of the world, megafossils have not been reported from Mexico, and unless there is other independent evidence, it is not possible to distinguish between dry grasslands, saline grasslands, páramo, or savanna grasses on the basis of pollen alone.

Mangrove

Avicennia, *Conocarpus*, **Laguncularia*, **Nypa* (extinct in New World), **Pelliceria* (extinct in Mexico), and **Rhizophora*, associated with ***Acrostichum* and **Hibiscus* (the pollen of *Hampea* is similar, but the association of this pollen type with mangroves suggests it is probably *Hibiscus*, and likely *H. tiliaceus*).

Beach/Strand/Dune

Batis, *Canavalia*, **Coccoloba*, *Ipomoea*, ***Iresine* (chenoam), ***Uniola* (Gramineae), associated with **Acacia*, *Caesalpinia*, **Casearia*, **Laguncularia*, **Palmae, ***Terminalia* (*Combretum–Terminalia*), **Tournefortia*.

Freshwater Herbaceous Bog/Marsh/Swamp

Bog: **Sphagnum*. Herbaceous broad-leaved marsh association: **Thalia*, associated with *Calathea*, *Heliconia*, **Pachira*, **Palmae (often fringing), and *Pontederia*.

Herbaceous reed-sedge marsh association: ***Phragmites* (Gramineae) and**Typha*, associated with **Cyperaceae (sedges) and Juncaceae (rushes).

Aquatic Vegetation

Ferns and allied groups: **Ceratopteris*, **Salvinia*. Angiosperms: *Cabomba*, *Ceratophyllum*, *Eichornia*, **Gramineae, *Lemna*, *Myriophyllum*, *Nymphoides*, *Pistia*, *Potamogeton*, **Sagittaria*, **Utricularia*, *Vallisneria*.

Lowland Neotropical Rain Forest

Bernoulia, **Bombax* (now treated as an African genus), *Brosimum*, *Calophyllum*, ***Combretum* (as *Combretum–Terminalia*), **Coussapoa*, **Crudia* (in New World South America north to Nicaragua; Mexico? riverine), *Dialium*, **Mortoniodendron*, *Pseudolmedia*, **Symphonia* (as *Pachydermites diederexi*).

Lower to Upper Montane Broad-Leaved Forest

Extensive: see Appendices 1.1 and 1.2. Deciduous forest association—Bryophyta: **Anthoceros* (moist places, widespread). Ferns and allied groups: **Alsophila*, **Anemia*, *Cnemidaria* (*Hemitelia*), **Cyathea*, *Dicranopteris*, **Lomariopsis*, *Lycopodium*, **Lygodium* (widespread), **Psilotum*, **Pteris*, **Selaginella* (widespread), **Sphaeropteris–Trichipteris*. Gymnosperm: **Podocarpus*. Angiosperms: *Acer*, **Alchornea*, **Alfaroa–Oreomunnea*, **Alnus*, **Allophylus*, **Borreria*, **Bravaisia*, **Bue(y)ttneria*, **Bursera* (widespread), *Carpinus*, **Carya*, **Cedrela* (to tropical), **Celtis*, *Clethra*, **Cleyera*, *Cornus*, ***Corylus* (often only as *Carpinus–Corylus–Ostrya*), **Cupania*, *Diospyros*, **Eucommia* (extinct in New World), ***Eugenia* (as *Eugenia–Myrcia*), **Fagus*, **Faramea* (moist), **Gramineae, **Guarea* (to tropical), **Gustavia*, **Hedyosmum*, *Heliconia*, **Heliocarpus* (to tropical), **Hiraea*, **Ilex*, **Juglans*, **Liquidambar*, *Magnolia*, **Meliosma*, **Myrica*, *Ostrya*, **Palmae, **Passiflora* (moist), **Persea*, **Platanus*, **Populus*, *Prunus*, **Quercus*, *Rhus*, *Rubus*, *Salix*, *Sambucus*, **Smilax*, **Spathiphyllum*, **Struthanthus* (e.g., oak woods), *Tapirira* (to tropical), **Ulmus*, *Weinmannia*.

Coniferous Forest

[*Araucaria*, Cretaceous, extinct in the Northern Hemisphere]

Pine, oak, and pine-oak associations: **Pinus*, *Cupressus*, *Juniperus*. Angiosperms: **Alnus*, ***Arbutus* (Ericaceae), *Buddleja*, *Cercocarpus*, *Crataegus*, *Fraxinus*, *Garrya*, **Juglans*, *Platanus*, **Populus*, **Quercus*, *Salix*.

Montane coniferous forest association: **Abies*, *Cupressus*, **Picea*, **Pinus*, *Pseudotsuga*, *Prunus*, **Quercus*.

Alpine Tundra (Páramo)

Arenaria, *Calamagrostis*, *Cerastium*, *Cirsium*, *Draba*, *Eryngium*, *Festuca*, *Gnaphalium*, **Gramineae, *Lupinus*, *Luzula*, *Muhlenbergia*, *Oxylobus*, *Phacelia*, *Plantago*, *Potentilla*, *Ranunculus*, *Senecio*, *Stipa*, *Trisetum* (possibly represented in the fossil record by some Gramineae and Compositae pollen unidentifiable to genus, but no prominent or defining members reported).

APPENDIX 1.4

Vegetation types used in this treatment (main headings), correlated with the potential natural vegetation types used by Borhidi (1996) for the vegetation of Cuba (subheadings). Roman numerals refer to Borhidi's numbering of vegetation types.

Desert

None (near deserts; driest phases of shrubland/chaparral–woodland–savanna).

Shrubland/Chaparral–Woodland–Savanna

IV. Tropical karst forests [vegetación de carso tropical (bosques de mogote)]
- West Cuban species-rich karstic forest (bosques carsicos del occidente de Cuba, ricos en especies)
- West Cuban species-poor karstic forest (bosques carsicos del occidente de Cuba, pobres en especies)
- Middle and east Cuban karstic forest (bosques carsicos del centro y este de Cuba)
- Montane karstic forest (bosques carsicos de mayor alturas)

V. Dry forests and shrubwoods [bosques arbustivos secos y espinosos (matorrales)]
- Dry evergreen forest (bosques arbustivos secos esclerófilos y espinosos)
- Dry thorny limestone shrubwoods (bosques arbustivos espinosos semideciduos sobre calizas)
- Dry thorny serpentine shrubwoods (bosques arbustivos espinosos esclerófilos sobre serpentinitas secas)
- Semi-dry evergreen shrubwoods (bosques arbustivos espinosos esclerófilos sobre serpentinitas semisecas)

VI. Semi-desert vegetation (vegetación semidesertica)
- Cactus scrub (matorrales abiertos secos con suculentas abundantes)

IX. Savannas (sabanas)
- *Roystonea–Ceiba* secondary savannas in the evergreen forest belt (sabanas secundarias de *Roystonea* y *Ceiba* en la habitad de bosques estacionales perennifolios)
- *Roystonea* secondary savannas in the semi-deciduous forest belt (sabanas secundarias de *Roystonea* en la habitad de bosques semideciduos mesófilos)
- *Copernicia* savannas with fluctuating water table (sabana de *Copernicia* con fluctuación del nivel freático en las habitades de bosques semideciduos micrófilos y espinosos)
- Seasonally wet and flooded *Sabal* savannas (sabanas de *Sabal* humedas o estacionalmente inundadas en las habitades de bosques aluviales y cenagosas)

Grassland

None.

Mangrove

XI (in part). Coastal vegetation (vegetación de costas marinas)

Beach/Strand/Dune

XI (in part). Coastal vegetation (vegetación de costas marinas)
- Sandy beaches (vegetación de costas arenosas)
- Littoral rock pavement (vegetación de costas rocosas)

Freshwater Herbaceous Bog/Marsh/Swamp

X. Freshwater vegetation (vegetación influida por la inundación)
- Alluvial and swamp forests [bosques con inundación estacional (bosque de pantano, bosque de ciénaga)]
- Riverain forests (bosques en galeria y bosques aluviales)
- Treeless swamp vegetation (herbazal de ciénaga)
- Freshwater weed vegetation (vegetación de aguas dulces)

Lowland Neotropical Rain Forest

None.

Lower to Upper Montane Broad-Leaved Forest

I. Rain forests or ombrophilous forests (pluvisilvas)
- Submontane rain forest (pluvisilvas submontanas)
- Wet montane rain forest (pluvisilvas montanas humedas)
- Semi-dry sclerophyllous montane rain forest on serpentine (pluvisilvas esclerófilas serpentinicolas)
- Elfin forest (bosques nublados o bosque enano)

II. Seasonal evergreen forests (bosques estacionales perennifolios)
- Lowland evergreen seasonal forest (bosques estacionales siempreverdes de llanuras)

Submontane evergreen seasonal forest (bosques estacionales siempreverdes submontanos)

III. Semi-deciduous forests (bosques semideciduos tropicales)

Mesophytic semi-deciduous forest (bosques semideciduos mesófilos)

Xerophytic semi-deciduous forest (bosques semideciduos micrófilos)

Coniferous Forest

Pine woods/savanna
Montane coniferous forest

APPENDIX 1.5

Representative taxa in the moist phase of the montane broad-leaved forest, Cuba (Sierra Rosario, Sierra Maestra). Names not in TROPICOS are those of Borhidi (1996).

Lower to Upper Montane Broad-Leaved Forest

Upper canopy (30–35 m)

Carapa guianensis, *Clusia rosea*.

Middle canopy (20–25 m)

Gymnosperm: *Podocarpus ekmanii*. Angiosperms: *Alchornea latifolia*, *Allophylus cominia*, *Andira inermis*, *Buchenavia capitata*, *Bursera simaruba*, *Calophyllum calaba*, *C. utile*, *Casearia hirsuta*, *Cedrela mexicana*, *Clusia tetrastigma*, *Cupania americana*, *C. glabra*, *Cyrilla racemiflora*, *Didymopanax morototoni*, *Diospyros crassinervis*, *Dipholis jubilla*, *D. salicifolia*, *Eugenia rhombea*, *E. maleolens*, *Faramea occidentalis*, *Ficus berteroi*, *F. crassinervia*, *F. wrightii*, *Garrya fadyenii*, *Gomidesia lindeniana*, *Guarea guidonia*, *Magnolia cubensis*, *Mastichodendron foetidissimum*, *Miconia punctata*, *Myrsine coriacea*, *Ocotea cuneata*, *O. floribunda*, *O. leucoxylon*, *Ossaea ottoschmidtii*, *Phoebe montana*, *Pithecellobium cubense*, *Roystonea regia*, *Sapium jamaicense*, *Sloanea curatellifolia*, *Tabebuia shaferi*, *Zanthoxylum cubense*, *Z. elephantiasis*, *Z. martinicense*, *Zizyphus rhodoxylon*, *Zuelania guidonia*.

Phases (clearings)—*Cecropia peltata*, *Didymopanax morototoni*, *Ochroma pyramidale*; (along creeks)—palms: *Bactris cubensis*, *Calyptronoma clementis*, *Prestoea montana*.

Lower canopy (6–15 m)

Ferns: *Alsophila aquilina*, *Cyathea araneosa*, *Hemitelia* (*Cnedidaria*) *horrida*. Angiosperms: *Brunellia comocladifolia*, *Chrysophyllum argenteum*, *Cordia sulcata*, *Dendropanax arboreus*, *Heliconia caribaea*, *Ilex macfadyenii*, *Lonchocarpus latifolius*, *Miconia dodecandra*, *M. elata*, *Oxandra* (*Sloanea*) *lanceolata*, *O. laurifolia*, *Sloanea amygdalina*, *Wallenia laurifolia*; lianas—*Celtis iguanaea*, *Gleichenia flexuosa*, *G. leonis*, *Lygodium volubile*, *Marcgravia evenia*, *Omphalea diandra*, *Smilax havanenesis*; epiphyte ferns *Elaphoglossum*, *Hymenophyllum*, and *Polypodium*, bromeliads, orchids; shrubs *Eugenia*, *Myrcia gundlachii*, *Rauvolfia salicifolia*; forest floor *Lycopodium*, other ferns, and several Compositae.

APPENDIX 1.6

Plant formations and representative tree/shrub and associated taxa in the vegetation of Jamaica. Community names in parentheses following the formation names are those of Aspery and Robbins (1953).

Desert

None (near deserts; driest phases of shrubland/chaparral–woodland–savanna).

Shrubland/Chaparral–Woodland–Savanna

(Dry limestone scrub forest; arid coastal faciation of dry limestone scrub forest; thorn scrub)

Acacia farnesiana, *A. lutea*, *A. tortuosa*, *A. villosa*, *Adelia ricinella*, *Albizia berteroana*, *Allophylus jamaicensis*, *Alternanthera ficoidea*, *Amyris elemifera*, *Annona squamosa*, *Batis maritima*, *Bauhinia divaricata*, *Bourreria succulenta*, *Bromelia pinguin*, *Brosimum alicastrum*, *Brya ebenus*, *Bumelia retusa*, *B. rotundifolia*, *Bursera simaruba*, *B. simplicifolia*, *Caesalpinia coriaria*, *C. vesicaria*, *Calyptranthes chytraculia*, *C. pallens*, *C. zuzygium*, *Canella winterana*, *Capparis cynophallophora*, *C. ferruginea*, *C. flexuosa*, *C. lanceolata*, *Casearia guianensis*, *Cassia emarginata*, *Cereus flagelliformis*, *C. peruvianus*, *C. triangularis*, *Chlorophora tinctoria*, *Chrysobalanus icaco*, *Citharexylum fruticosum*, *Clusia flava*, *Coccoloba krugii*, *Coccothrinax fragrans*, *Colubrina reclinata*, *Comocladia velutina*, *Cordia geraschanthoides*, *C. nitida*, *C. sebestena*, *Crescentia cujete*, *Croton glabellus*, *C. linearis*, *Diospyros tetrasperma*, *Erythroxylum areolatum*, *E. rotundifolium*, *Eugenia axillaris*, *E. monticola*, *Exothea paniculata*, *Exostema caribaeum*, *Guaiacum officinale*, *Guazuma ulmifolia*, *Gymnanthes lucida*, *Haematoxylum campechianum*, *Hippomane mancinella*, *Hypelate trifoliata*, *Jacquinia armillaris*, *Krugiodendron ferreum*, *Linociera ligustrina*, *Matayba apetala*, *Melicoccus bijugatus*, *Melocactus communis*, *Ocotea jamaicensis*, *Opuntia spinosissima*, *O. tuna*, *Oxandra lanceolata*, *Peltophorum brasiliense*, *Phyllanthus acuminatus*, *Picrodendron baccatum*, *Piscidia piscipula*, *Pisonia fragrans*, *P. obtusata*, *Pithecellobium unguis-cati*, *Plumeria alba*, *Prosopis juliflora*, *Rhamnidium jamaicense*, *Rhus metopium*, *Sarcomphalus laurinus*, *Sapota sideroxylon*, *Sideroxylon foetidissimum*, *Swietenia mahogoni*, *Tecoma leucoxylon*, *Thrinax parviflora*, *Tillandsia balbisiana*, *T. recurvata*, *Ximenia americana*, *Zanthoxylum fagara*, *Z. spinosum*.

Grassland

None.

Mangrove

(Mangrove woodland)

Acrostichum aureum, *Avicennia nitida*, *Conocarpus erecta*, *Laguncularia racemosa*, *Rhizophora mangle*.

Beach/Strand/Dune

Acacia tortuosa, *Batis maritima*, *Coccoloba uvifera*, *Conocarpus erecta*, *Cordia sebestena*, *Ipomoea pes-caprae*, *Jatropha gossypiifolia*, *Opuntia tuna*, *Pithecellobium unguis-cati*, *Prosopis juliflora*, *Sesuvium portulacastrum*, *Sporobolus virginicus*, *Thrinax parviflora*, *Tournefortia gnaphalodes*, *Uniola virgata*.

Freshwater Bog/Marsh/Swamp

(Herbaceous swamp, marsh forest; palm-sedge)

Arundo donax, *Calophyllum jacquinii*, *Calyptronoma swartzii*, *Cyperus giganteus*, *Echinodorus* sp., *Eleocharis* sp., *Ficus* sp., *Grias caulifera*, *Haematoxylum campechianum*, *Mariscus jamaicensis*, *Phragmites communis*, *Piscidia piscipula*, *Roystonea princeps*, *Spondias mombin*, *Symphonia globulifera*, *Terminalia latifolia*, *Typha angustifolia*.

Aquatic

Fern: *Azolla caroliniana*. Angiosperms: *Ceratophyllum demersum*, *Eichornia crassipes*, *Hydrocotyle umbellata*, *Lemna minor*, *Myriophyllum* sp., *Nymphaea alba*, *Pistia stratiotes*, *Potamogeton* sp., *Sagittaria* sp., *Utricularia stellaris*.

Lowland Neotropical Rain Forest

None.

Lower to Upper Montane Broad-Leaved Forest

(Wet limestone forest, lower shale hills, lower montane rain forest, montane sclerophyll, montane mist, elfin woodland)

Ferns: *Alsophila aspera*, *A. swartziana*, *Anemia hirsuta*, *A. underwoodiana*, *Asplenium pumilum*, *Blechnum unilaterale*, *Campyloneurum angustifolium*, *Ctenitis ampla*, *C. effusa*, *C. villosa*, *Cyathea grevilleana*, *C. tussacii*, *Dennstaedtia bipinnata*, *D. cicutaria*, *Dryopteris pedata*, *D. resinifera*, *Gymnopteris rufa*, *Lomariopsis underwoodii*, *Lygodium volubile*, *Notholaena trichomanoides*, *Polypodium dissimile*, *P. heterophyllum*, *Polystichum christianae*, *Pteris quadriaurita*, *Thelypteris asterothrix*, *T. patens*, *T. sagittata*, *T. serrulata*, *T. venusta*, *Trichomanes* sp., *Trismeria trifoliata*. Gymnosperm: *Podocarpus urbanii*. Angiosperms: *Acnistus arborescens*, *Alchornea latifolia*, *Amyris balsamifera*, *Andira inermis*, *Antirrhoea* (*Antirhea*) *jamaicensis*, *Baccharis scoparia*, *Bauhinia divaricata*, *Blakea trinervia*, *Bocconia frutescens*, *Brosimum alicastrum*, *Brunellia comocladifolia*, *Brya ebenus*, *Buchenavia capitata*, *Bursera simaruba*, *Byrsonima coriacea*, *Calophyllum jacquinii* (*C. brasiliense*), *Calyptronoma swartzii*, *Cecropia peltata* (open, disturbed habitats), *Cedrela odorata*, *Ceiba pentandra*, *Celtis trinervia*, *Chlorophora tinctoria*, *Chrysophyllum oliviforme*, *Clethra alexandri*, *C. occidentalis*, *Clusia havetioides*, *C. rosea*, *Coccoloba laurifolia*, *Colubrina ferruginosa*, *Comocladia pinnatifolia*, *Cordia geraschanthoides*, *Crescentia cujete*, *Cyrilla racemiflora*, *Dipholis nigra*, *Dodonaea viscosa*, *Drypetes lateriflora*, *Eugenia alpina*, *E. axillaris*, *E. biflora*, *E. disticha*, *E. fragrans*, *E. monticola*, *Exothea paniculata*, *Ficus harrisii*, *F. suffocans*, *F. wilsoni*, *Gilibertia* (*Quivisia*) *arborea*, *G. nutans*, *Guarea glabra*, *Guazuma ulmifolia*, *Guettarda argentia*, *Hedyosmum arborescens*, *Hernandia catalpifolia*, *Heteropteris laurifolia*, *Hufelandia pendula*, *Hura crepitans*, *Ilex montana*, *Lagetta lagetto*, *Lucuma mammosa*, *Matayba apetala*, *Mimusops excisa*, *Misanteca triandra*, *Mosquitoxylum jamaicense*, *Nectandra antillana*, *N. coriacea*, *N. patens*, *N. sanguinea*, *Ochroma pyramidale*, *Ocotea martinicensis*, *O. staminea*, *Oxandra* (*Sloanea*) *lanceolata*, *O. laurifolia*, *Palicourea crocea*, *Persea alpigena*, *Picranea antidesma*, *P. excelsa*, *Pimenta officinalis*, *Pithecellobium arboreum*, *Prunus myrtifolia*, *P. occidentalis*, *Psidium montanum*, *Rondeletia* sp., *Sapium jamaicense*, *Sciadophyllum brownii*, *Senecio discolor*, *Simaruba glauca*, *Sloanea jamaicensis*, *Spathelia glabrescens*, *S. sorbifolia*, *Spondias mombin*, *S. purpurea*, *Symphonia globulifera*, *Trema micrantha*, *Trophis racemosa*, *Vaccinium meridionale*, *Viburnum villosum*, *Weinmannia pinnata*, *Xylopia muricata*, *Zanthoxylum flavum*, *Z. martinicense*, *Zizyphus chloroxylon*.

Coniferous Forest

None (highest altitudes, e.g., Blue Mountains, occupied by *Podocarpus urbani*/*Cyrilla racemiflora* forest with elfin forest aspect).

Alpine Tundra (Páramo)

None.

APPENDIX 1.7

Dominant or characteristic plants of the Parc National Pic Macaya and the Parc National La Visite, Haiti. Community names in parentheses following formation names are those of Judd (1987).

Parc National Pic Macaya

Coniferous Forest/Montane Broad-Leaved Forest

(Pine forest–cloud forest)

[Species marked with a (+) also occur in the moist limestone forest below]

Ferns: +*Alsophila hotteana*, *A. minor*, *Blechnum tuerckheimii*, *B. underwoodianum*, *Culcita coniifolia*, *Cyathea harrisii*, *Gleichenia* sp., *Histiopteris incisa*, *Lophosoria quadripinnata*, *Pteridium aquilinum*. Gymnosperm: *Pinus occidentalis*. Angiosperms: *Agave antillarum*,

+Ardisia fuertesii, *Arthrostylidium haitiense*, *Baccharis myrsinites*, *Banara splendens*, *+Besleria lutea*, *Brunellia comocladifolia*, *Calyptranthes hotteana*, *C. nummularia*, *Cestrum coelophlebium*, *C. filipes*, *Citharexylum caudatum*, *+Daphnopsis crassifolia*, *+Dendropanax arboreus*, *D. stellatus*, *+Didymopanax tremulus*, *Eugenia formonica*, *Eupatorium flavidulum*, *E. urbanii*, *Fuchsia pringsheimii*, *Garrya fadyenii*, *Gyrotaenia myriocarpa*, *Haenianthus oblongatus*, *Henrietta barkeri*, *Heterotrichum umbellatum*, *Hyptis schusteri*, *Ilex macfadyenii*, *I. obcordata*, *Illicium ekmanii*, *+Lobelia robusta*, *L. rotundifolia*, *Meriania* sp., *Miconia apiculata*, *M. barkeri*, *M. hypiodes*, *M. ossaeifolia*, *+M. subcompressa*, *M. tetrastoma*, *Myrica picardae*, *Myrsine coriacea*, *Ocotea foeniculacea*, *Pachyanthus cubensis*, *+Palicourea alpina*, *Persea anomala*, *Pluchea symphytifolia*, *Psychotria alpestris*, *P. liogieri*, *Rhytidophyllum auriculatum*, *Rondeletia formonia*, *Rubus* sp., *Sapium haitiense*, *+Senecio stenodon*, *Solanum formonense*, *S. hotteanum*, *Symplocos hotteana*, *Tabebuia berteroi*, *Ternstroemia barkeri*, *Trema micrantha*, *Trichilia havanensis*, *Vaccinium racemosum*, *Vernonia buxifolia*, *+V. saepium*, *Weinmannia pinnata*, *+Zanthoxylum haitiense*.

(Moist limestone forest)

Ferns: *Cnemidaria horrida*, *Cyathea furfuracea*. Angiosperms: *Alchornia latifolia*, *Allophylus crassinervis*, *Amyris apiculata*, *Beilschmiedia pendula*, *Brunfelsia picardae*, *Calycogonium apiculatum*, *C. calycopteris*, *Calyptranthes sintenisii*, *Casearia sylvestris*, *Cecropia peltata*, *Cestrum bicolor*, *C. picardae*, *Chrysophyllum argenteum*, *Clusia clusioides*, *Coccothrinax* cf. *montana*, *Comocladia pinnatifolia*, *Cupania americana*, *Daphnopsis americana*, *Dipholis cubensis*, *Eugenia christii*, *E. glabrata*, *Eupatorium microchaeteum*, *E. nervosum*, *E. stigmaticum*, *Ficus citrifolia*, *Garcinia barkeriana*, *Gesneria* sp., *Guarea guidonia*, *Gymnanthes lucida*, *Heliconia bihai*, *Jacquinea eggersii*, *Lunania mauritii*, *Maytenus hotteana*, *Mecranium haitiense*, *M. microdictyum*, *M. revolutum*, *Meliosma recurvata*, *Miconia laevigata*, *Micropholis polita*, *Nectandra membranacea*, *N. patens*, *Ossaea setulosa*, *Phoebe* cf. *montana*, *Phyllanthus myriophyllus*, *Piper confusum*, *P. hispidum*, *Pithecellobium oppositifolium*, *Polygala penaea*, *Prunus myrtifolia*, *P. occidentalis*, *Psychotria berteroana*, *P. pubescens*, *Rhytidophyllum bicolor*, *Salvia* sp., *Solanum antillarum*, *S. erianthum*, *S. torvum*, *Tabebuia conferta*, *Turpinia picardae*, *Zanthoxylum haitiense*, *Z. martinicense*.

Parc National La Visite

(Pine forest)

Ferns: *Blechnum occidentale*, *Campyloneurum angustifolium*, *Lophosoria quadripinnata*, *Pteridium aquilinum*, *Woodsia montevidensis*. Gymnosperm: *Pinus occidentalis*. Angiosperms: *Agave antillarum*, *Baccharis myrsinites*, *Bocconia frutescens*, *Bumelia subintegra*, *Cestrum mononeurum*, *Daphnopsis crassifolia*, *Eupatorium cabaionum*, *E. illitum*, *Fuchsia pringsheimii*, *F. triphylla*, *Garrya fadyenii*, *Gesneria bullata*, *Hypericum hypericoides*, *Ilex macfadyenii*, *Lyonia microcarpa*, *L. rubiginosa* var. *costata*, *L. truncata*, *Myrica picardae*, *Myrsine coriacea*, *Oreopanax capitatus*, *Persea anomala*, *Salvia selleana*, *Solanum crotonoides*.

(Cloud forest/Moist hardwood)

Ferns: *Alsophila minor*, *Cyathea harrisii*. Gymnosperms: *Juniperus ekmanii*, *Podocarpus aristulatus*. Angiosperms: *Agave antillarum*, *Ardisia fuertesii*, *A. picardae*, *Brunellia comocladifolia*, *Buddleja domingensis*, *Bumelia subintegra*, *Bunchosia ekmanii*, *Calyptranthes densifolia*, *C. pitoniana*, *Cestrum brevifolium*, *C. coelophlebium*, *C. inclusum*, *C. mononeurum*, *Citharexylum caudatum*, *Coccoloba picardae*, *Cordia dependens*, *C. picardae*, *Daphnopsis crassifolia*, *Datura suaveolens*, *Dendropanax arboreum* (*D. arboreus*), *Didymopanax tremulus*, *Duranta arida*, *Eugenia picardae*, *Eupatorium cabaionum*, *E. illitum*, *Garrya fadyenii*, *Gesneria bullata*, *G. ekmanii*, *G. viridiflora*, *Gyrotaenia myriocarpa*, *Heterotrichum umbellatum*, *Ilex macfadyenii*, *Lobelia assurgens*, *L. robusta*, *L. rotundifolia*, *Lyonia buchii*, *L. microcarpa*, *Malpighia macracantha*, *Mecranium multiflorum*, *Meliosma impressa*, *Meriania involucrata*, *Miconia favosa*, *M. ferruginata*, *M. selleana*, *M. tetrastoma*, *Myrica picardae*, *Myrsine coriacea*, *M. nubicola*, *Ocotea acarina*, *O. wrightii*, *Oreopanax capitatus*, *Persea anomala*, *Picramnia selleana*, *Prestoea montana*, *Psychotria baltenweckii*, *Rhytidophyllum auriculatum*, *Rondeletia carnea*, *R. christii*, *R. domatiata*, *Salvia foveolata*, *S. tuerckheimii*, *Sapium buchii*, *Satureja viminea*, *Senecio buchii*, *S. picardae*, *Siphocampylus caudatus*, *Solanum crotonoides*, *S. umbellatum*.

APPENDIX 1.8

Tree communities of Puerto Rico according to the systems of Little and Wadsworth (1964) and the one used in the present text.

Mangrove

[mentioned in Little & Wadsworth (1964) but not included on their map; Fig. 3.72]

Avicennia nitida, *Conocarpus erectus*, *Laguncularia racemosa*, *Rhizophora mangle*.

Beach/Strand/Dune

[mentioned in Little & Wadsworth (1964) but not included on their map; Fig. 3.72]

Coccoloba uvifera.

Shrubland/Chaparral–Woodland–Savanna

(Dry coastal forest)

Bucida buceras, *Canella winterana*, *Capparis cynophallophora*, *Ceiba pentandra*, *Citharexylum fruticosum*, *Coccoloba venosa*, *Cordia nitida*, *Erythroxylum areolatum*, *Guaiacum officinale*, *Guazuma ulmifolia*, *Lonchocarpus domingensis*, *Pictetia aculeata*, *Polygala cowellii*, *Rauvolfia nitida*, *Stahlia monosperma*.

(Dry limestone forest)

Amyris elemifera, *Bucida buceras*, *Bursera simaruba*, *Capparis cynophallophora*, *Cephalocereus royenii*, *Colubrina arborescens*, *Dipholis salcifolia*, *Guaiacum officinale*, *G. sanctum*, *Gymnanthes lucida*, *Opuntia rubescens*, *Pictetia aculeata*, *Pisonia albida*, *Plumeria alba*, *Sarcomphalus reticulatus*, *Thouinia portoricensis*.

Lower to Upper Montane Broad-Leaved Forest

(Moist coastal forest)

Acrocomia media, *Andira inermis*, *Calophyllum brasiliense*, *Citharexylum fruticosum*, *Genipa americana*, *Guettarda scabra*, *Hernandia sonora*, *Hymenaea courbaril*, *Mammea americana*, *Manilkara bidentata*, *Nectandra coriacea*, *Petitia domingensis*, *Psidium guajava*, *Pterocarpus officinalis*, *Randia aculeata*, *Sideroxylon foetidissimum*, *Tabebuia heterophylla*, *Zanthoxylum martinicense*.

(Moist limestone forest)

Aiphanes acanthophylla, *Bucida buceras*, *Bursera simaruba*, *Cedrela odorata*, *Clusia rosea*, *Coccoloba diversifolia*, *C. pubescens*, *Dipholis salicifolia*, *Gaussia attenuata*, *Guettarda scabra*, *Hyeronima clusioides*, *Licaria salicifolia*, *Montezuma speciosissima*, *Ochroma pyramidale*, *Randia aculeata*, *Sapium striata*, *Sideroxylon foetidissimum*, *Terebraria resinosa*, *Tetrazygia eleagnoides*, *Thouinia striata*, *Zanthoxylum martinicense*.

(Lower cordillera forest)

Fern: *Cyathea arborea*. Angiosperms: *Andira inermis*, *Buchenavia capitata*, *Byrsonima coriacea*, *Casearia arborea*, *Cecropia peltata*, *Cedrela odorata*, *Cordia alliodora*, *C. borinquensis*, *C. sulcata*, *Cupania americana*, *Dacryodes excelsa*, *Dendropanax arboreus*, *Didymopanax morototoni*, *Drypetes glauca*, *Guarea trichilioides* (*G. grandiflora*), *Hirtella rugosa*, *Homalium racemosum*, *Inga laurina*, *Linociera domingensis*, *Meliosma herbertii*, *Myrcia deflexa*, *Ocotea leucoxylon*, *O. moschata*, *Ormosia krugii*, *Pithecellobium arboreum*, *Tabebuia heterophylla*, *Vitex divaricata*.

(Upper cordillera forest)

Fern: *Cyathea arborea*. Gymnosperm: *Podocarpus coriaceus*. Angiosperms: *Alchornea latifolia*, *Brunellia comocladifolia*, *Calycogonium squamulosum*, *Clusia krugiana*, *Euterpe globosa*, *Guatteria blainii*, *Heterotrichum cymosum*, *Magnolia portoricensis*, *Matayba domingensis*, *Micropholis chrysophylloides*, *Ocotea spathulata*, *Turpinia paniculata*, *Weinmannia pinnata*.

(Lower Luquillo forest)

Fern: *Cyathea arborea*. Angiosperms: *Alchorneopsis portoricensis*, *Andira inermis*, *Beilschmiedia pendula*, *Buchenavia capitata*, *Byrsonima coriacea*, *Casearia arborea*, *Cecropia peltata*, *Cordia borinquensis*, *Cupania americana*, *Dacryodes excelsa*, *Drypetes glauca*, *Guarea trichilioides* (*G. grandiflora*), *Hirtella rugosa*, *Inga laurina*, *Linociera domingensis*, *Manilkara bidentata*, *Meliosma herbertii*, *Myrcia deflexa*, *Ochroma pyramidale*, *Ocotea leucoxylon*, *O. moschata*, *Ormosia krugii*, *Sapium laurocerasus*, *Sloanea berteroana*, *Tabebuia heterophylla*, *Tetragastris balsamifera*, *Trichilia pallida*.

(Upper Luquillo forest)

Fern: *Cyathea arborea*. Angiosperms: *Alchornea latifolia*, *Calycogonium squamulosum*, *Calyptranthes krugii*, *Clusia krugiana*, *Croton poecilanthus*, *Cyrilla racemiflora*, *Eugenia borinquensis*, *Euterpe globosa*, *Heterotrichum cymosum*, *Magnolia splendens*, *Matayba domingensis*, *Micropholis chrysophylloides*, *M. garciniifolia*, *Ocotea spathulata*, *Tabebuia rigida*.

APPENDIX 1.9

Summary of the principal genera mentioned in the text that characterize the plant communities of the Greater Antilles, including representatives in the microfossil record. An asterisk (*) indicates the genus has been identified from the Tertiary of the Greater Antilles (Quaternary occurrences are listed in Table 5.1). A double asterisk (**) indicates the genus may be present, but the fossil(s) can be referred only to a broader taxonomic category (viz., group of genera, family, or group of families). Taxa may range through more than one formation, and some may have changed associations from Cretaceous through ~middle Eocene times (see I: pp. 124, 332).

Desert

None (near deserts; included here in the driest phases of shrubland/chaparral–woodland–savanna formation).

Shrubland/Chaparral–Woodland–Savanna

Fern: **Alsophila*. Gymnosperm: **Pinus*. Angiosperms: **Acacia*, *Acidoton*, *Acrosynanthus*, *Agave*, *Albizia*, *Allophylus*, *Alternanthera*, *Amyris*, *Annona*, *Antirhea*, *Ateelia*, *Ateramnus*, *Auerodendron*, *Batis*, *Bauhinia*, *Belairia*, *Bombacopsis*, *Bourreria*, *Bromelia*, *Brosimum*, *Brya*, *Bucida*, *Bumelia*, *Bursera*, *Byrsonima*, *Caesalpinia*, *Calliandra*, *Calyptranthes*, *Canella*, *Capparis*, *Casearia*, *Cassia*, *Ceiba*, *Cephalocereus*, *Cereus*, *Chlorophora*, *Chrysobalanus*, *Citharexylum*, *Clusia*, *Coccoloba*, *Coccothrinax*, *Colubrina*, *Comocladia*, *Copernicia*, *Cordia*, *Crescentia*, *Croton*, *Curatella*, *Cyrilla*, *Diospyros*, *Dipholis*, *Erithalis*, *Erythroxylum*, *Eugenia*, *Exostema*, *Exotheca*, *Garcinia*, *Gaussia*, *Gossypiospermum*, *Guaiacum*, *Guazuma*, *Guettarda*, *Gymnanthes*, *Haematoxylum*, *Hauya* (to more moist), *Hippomane*, *Hypelate*, *Ilex*, *Illicium*, **Jacaranda*, *Jacquinia*, *Jatropha*, *Krugiodendron*, *Laplacea*, *Leptocereus*, *Linociera*, *Lonchocarpus*, *Lyonia*, *Machaerina*, *Manilkara*, *Matayba*, *Maytenus*, *Melicoccus*, *Melocactus*, *Moacroton*, *Myrica*, *Ocotea*, *Opuntia*, *Oxandra*, *Pedilanthus*, *Peltophorum*, *Phyllanthus*, *Phyllostylon*, *Picrodendron*, *Pictetia*, *Pilocereus*, *Piscidia*, *Pisonia*, *Pithecellobium*, *Plumeria*, *Polygala*, *Prosopis*, *Pseudocarpidium*, *Psychotria*, *Rauvolfia*, *Rhamnidium*, *Rhipsalis*, *Rhus*, *Ritterocereus*,

Rondeletia, *Roystonea*, *Sabal*, *Sarcomphalus*, *Sapota*, *Selenicereus*, *Sideroxylon*, *Spirotecoma*, *Sporobolus*, *Stahlia*, *Swietenia*, *Tabebuia*, *Tabernaemontana*, *Tapura*, *Tecoma*, *Thouinia*, *Thrinax*, *Tillandsia*, *Ximenia*, *Xylosma*, *Zanthoxylum*.

Grasslands

None (mostly anthropogenic).

Mangrove

Fern: *Acrostichum*. Angiosperms: *Avicennia*, *Caesalpinia*, *Conocarpus*, *Dalbergia*, *Drepanocarpus*, *Hibiscus*, *Laguncularia*, *Malache*, **Pelliceria* (no longer present in the Antilles), *Piscidia*, *Pterocarpus*, **Rhizophora*, *Ximenia*.

Beach/Strand/Dune

Gymnosperms: *Microcycas*, *Zamia*. Angiosperms: *Acacia*, *Achyranthes*, *Agave*, *Annona*, *Atriplex*, *Baccharis*, *Batis*, *Bef(j)aria*, *Bontia*, *Borrichia*, *Caesalpinia*, *Canavalia*, *Capparis*, *Catesbaea*, *Cenchrus*, *Chrysobalanus*, *Cnidoscolus*, *Coccoloba*, *Colubrina*, *Comocladia*, *Conocarpus*, *Cordia*, *Distichilis*, *Dodonaea*, *Erithalis*, *Ernoea*, *Eugenia*, *Euphorbia*, *Flaveria*, *Guettarda*, *Gymnanthes*, *Heliotropium*, *Hippomane*, *Ipomoea*, *Jacquinia*, *Jatropha*, *Kalmia*, *Lachnocaulon*, *Lantana*, *Lechea*, *Lithophila*, *Melocactus*, *Metopium*, *Opuntia*, *Pectis*, *Phyllanthus*, *Phylostylon*, *Pieria*, *Pilocereus*, *Pithecellobium*, *Portulaca*, *Prosopis*, *Quercus*, *Rachicallis*, *Randia*, *Reynosia*, *Salicornia*, *Scaevola*, *Sesuvium*, *Spartina*, *Sporobolus*, *Strumpfia*, *Suaeda*, *Suriana*, *Swietenia*, *Tabebuia*, *Terminalia*, *Thespesia*, *Thrinax*, *Tournefortia*, *Trianthema*, *Turnera*, *Uniola*, *Victoria*.

Freshwater Herbaceous Bog/Marsh/Swamp

Acoelorraphe, *Annona*, *Arundo*, *Ascarum*, *Bucida*, *Caladium*, *Calophyllum*, *Calyptronoma*, *Chrysobalanus*, *Coccothrinax*, *Cyperus*, *Drosera*, *Echinodorus*, *Eleocharis*, *Ficus*, *Fraxinus*, *Gerardia*, *Haematoxylum*, *Hibiscus*, *Lobelia*, *Mariscus*, *Nuphar*, *Nymphaea*, *Phragmites*, *Piscidia*, *Pistia*, *Polygonum*, *Potentilla*, *Rhynchospora*, *Roystonea*, *Sabal*, *Sagittaria*, *Salix*, *Scirpus*, *Sisyrinchium*, *Solidago*, *Spondias*, *Stellaria*, *Symphonia*, *Tabebuia*, *Terminalia*, *Thalia*, *Typha*, *Valisneria*, *Vicia*.

Aquatic

Fern: *Azolla*. Angiosperms: *Brasenia*, *Cabomba*, *Ceratophyllum*, *Eichornia*, *Hydrocotyle*, *Lemna*, *Limnocharis*, *Myriophyllum*, *Najas*, *Nelumbo*, *Nuphar*, *Nymphaea*, *Nymphoides*, *Pistia*, *Polygonum*, *Potamogeton*, *Sagittaria*, *Utricularia*, *Valisneria*.

Lowland Neotropical Rain Forest

None (remnants included here in wettest phase of montane broad-leaved forest formation; lower montane wet forest).

Lower to Upper Montane Broad-Leaved Forest

Ferns and allied groups: *Alsophila*, *Anemia*, *Asplenium*, *Blechnum*, *Campyloneurum*, *Cnemidaria*, *Ctenitis*, *Culcita*, *Cyathea*, *Dennstaedtia*, *Dryopteris*, *Elaphoglossum*, **Eriosorus–Jamesonia*, *Gleichenia*, *Gymnopteris*, *Hemitelia* (*Cnemidaria*), *Histiopteris*, *Hymenophyllum*, *Lomariopsis*, *Lophosoria*, **Lycopodium*, *Lygodium*, *Notholaena*, *Odontosoria*, *Polypodium*, *Polystichum*, *Pteridium*, **Pteris*, **Selaginella*, *Thelypteris*, *Trichomanes*, *Trismeria*, *Woodsia*. Gymnosperms: *Juniperus*, **Podocarpus*. Angiosperms: *Acnistus*, *Acoelorraphe*, *Acrocomia*, *Agave*, *Aiphanes*, **Alchornea* (to moist), *Alchorneopsis*, **Alfaroa–Oreomunnea* (extinct in the Antilles), *Allophylus*, *Amyris*, *Andira*, *Antirrhoea*, *Ardisia*, *Arthrostylidium*, *Baccharis*, *Bactris*, *Banara*, *Bauhinia*, *Beilschmiedia*, **Bernoulia*, *Besleria*, *Blakea*, *Bocconia*, **Bombax*, *Brosimum*, **Brunellia*, *Brunfelsia*, *Brya*, *Buchenavia*, *Bucida*, *Buddleja*, *Bumelia*, *Bunchosia*, *Bursera*, *Byrsonima*, *Calophyllum*, *Calycogonium*, *Calyptranthes*, *Calyptronoma*, *Carapa*, **Casearia* (to dry), *Cecropia* (disturbed), *Cedrela*, *Ceiba*, *Celtis*, *Cestrum*, *Charianthus*, *Chlorophora*, **Chrysophyllum*, *Citharexylum*, *Clethra*, *Clusia*, *Coccoloba*, *Coccothrinax*, *Colubrina*, *Comocladia*, *Conocarpus*, *Cordia*, *Crescentia*, *Croton*, *Cupania*, *Cyrilla*, *Dacryodes*, *Dalbergia*, *Daphnopsis*, *Datura*, **Dendropanax*, *Didymopanax* (disturbed), *Diospyros*, *Dipholis*, *Dodonaea*, *Drypetes*, *Duranta*, *Elaphrium*, *Eugenia*, *Eupatorium*, *Euterpe*, *Exotheca*, **Faramea*, *Ficus*, *Fraxinus*, *Freziera*, *Fuchsia*, *Garcinia*, *Garrya*, *Gaussia*, *Genipa*, *Gesneria*, *Gilibertia* (*Quivisia*), *Ginoria*, *Gomidesia*, *Guaiacum*, **Guarea*, *Guatteria*, *Guazuma*, *Guettarda*, *Gymnanthes*, *Gyrotaenia*, *Haenianthus*, *Hedyosmum*, *Heliconia*, *Hernandia*, *Henrietta*, *Heteropteris*, *Heterotrichum*, *Hibiscus*, *Hirtella*, *Homalium*, *Hufelandia*, *Hura*, *Hye(i)ronima*, *Hymenaea*, *Hypericum*, *Hyptis*, *Ilex*, *Illicium*, *Inga*, *Jacquinia*, *Juglans*, *Lagetta*, *Licaria*, *Linociera*, *Lobelia*, *Lonchocarpus*, *Lucuma*, *Luehea*, *Lunania*, *Lyonia*, *Lysiloma*, *Magnolia*, *Malpighia*, *Mammea*, *Manilkara*, *Marcgravia* (moist), *Mastichodendron*, *Matayba*, *Maytenus*, *Mecranium*, *Meliosma*, *Meriania*, *Miconia*, *Micropholis*, *Mimusops*, *Misanteca*, *Montezuma*, *Mosquitoxylum*, *Myrcia*, *Myrica*, *Myrsine*, *Nectandra*, *Ochroma* (disturbed), *Ocotea*, *Omphalea*, *Oreopanax*, *Ormosia*, *Ossaea*, *Oxandra*, *Pachyanthus*, *Palicourea*, *Peltophorum*, *Persea*, *Petitia*, *Phoebe*, *Phyllanthus*, *Picramnia*, *Pimenta*, *Piper*, *Pithecellobium*, *Pleodendron*, *Pluchea*, *Polygala*, *Prestonia*, *Prunus*, *Psidium*, *Psychotria*, *Pterocarpus*, *Quercus*, *Randia*, **Rauvolfia*, *Rhytidophyllum*, *Richeria*, *Rondeletia*, *Roystonea*, *Rubus*, *Sabal*, **Salix*, *Salvia*, *Samanea*, *Sapium*, *Satureja*, *Sciadophyllum*, *Senecio*, *Sideroxylon*, *Simaruba*, *Siphocampylus*, *Sloanea*, *Smilax*, *Solanum*, *Spathelia*, *Spondias*, *Swietenia*, *Symphonia*, *Symplocos*, *Tabebuia*, *Tabernaemontana*, *Terebraria*, *Ternstroemia*, *Tetragrastis*, *Tetrazygia*, *Thouinia*, *Torralbasia*, *Tournefortia*, *Trema*, *Trichilia*, *Trophis*, *Turpinia*, *Vaccinium*, *Vernonia*, *Viburnum*, *Vitex*, *Wallenia*, *Weinmannia*, *Xylopia*, **Zanthoxylum*, *Zizyphus*, *Zuelania*.

Coniferous Forest

Gymnosperms: *Pinus* (*Podocarpus* in elfin forest). Angiosperms: *Byrsonima*, *Colpothrinax*, *Curatella*, *Panicum*, *Quercus* (a number of plants from the intermixed cloud forest of Haiti range into the pine forest; see Appendix 1.7).

Alpine Tundra (Páramo)

None.

APPENDIX 1.10

Plant formations with principal genera comprising the vegetation of Guatemala. Community names in parentheses are those used by Standley and Steyermark (1945).

Shrubland/Chaparral–Woodland–Savanna

(Petén plains, low savanna, Pacific plains forest, desert–chaparral)

Acacia, *Acanthocereus*, *Aristida*, *Achras*, *Andropogon*, *Bacopa*, *Bouteloua*, *Brosimum*, *Bursera*, *Byrsonima*, *Calophyllum*, *Cassia*, *Ceiba*, *Cephalocereus*, *Cochlospermum*, *Conobea*, *Crescentia*, *Crumenaria*, *Cryosophila*, *Curatella*, *Diodia*, *Echinodorus*, *Erythroxylum*, *Evolvulus*, *Ficus*, *Fimbristylis*, *Gliricidia*, *Gomphrena*, *Jacquinia*, *Juliania*, *Karwinskia*, *Lemaireocereus*, *Limnobium*, *Lucuma*, *Pacourina*, *Panicum*, *Pereskia*, *Phoradendron*, *Piper*, *Portulaca*, *Psychotria*, *Rheedia*, *Ruprechtia*, *Scleria*, *Sida*, *Sterculia*, *Swietenia*, *Tabebuia*, *Talinum*.

Mangrove

Acrostichum, *Avicennia*, *Conocarpus*, *Laguncularia*, *Rhizophora*.

Beach/Strand/Dune

Canavalia, *Ipomoea*, *Sesuvium*.

Freshwater Herbaceous Bog/Marsh/Swamp

Ferns: *Acrostichum*, *Blechnum*, *Dryopteris*, *Nephrolepis*. Angiosperms: Cyperaceae (*Cyperus*, *Eleocharis*, *Fuirena*, *Scleria*), Gramineae (*Andropogon*, *Phragmites*), *Ludwigia*, *Pachira*, *Polygonum*, *Thalia*, *Typha*.

Aquatic

Fern: *Ceratophyllum*. Angiosperms: *Cabomba*, *Eichornia*, *Lemna*, *Myriophyllum*, *Najas*, *Nymphaea*, *Nymphoides*, *Pistia*, *Pontederia*, *Potamogeton*, *Sagittaria*, *Utricularia*.

Lowland Neotropical Rain Forest

(Atlantic Rain Forest)

Andira, *Bauhinia*, *Calocarpum*, *Calyptrogenia*, *Chrysophyllum*, *Entada*, *Ficus*, *Hexopetion*, Palmae (*Calyptrogyne*, *Chamaedorea*, *Orbignya*).

Lower to Upper Montane Broad-Leaved Forest

(Alta Verapaz wet forest, Pacific Boca Costa forest)

Gymnosperms: *Ceratozamia*, *Podocarpus*, *Taxus*. Angiosperms: *Alfaroa–Oreomunnea* (*Engelhardia*), *Berchemia*, *Billia*, *Calocarpum*, *Cestrum*, *Cheiranthodendron*, *Dahlia*, *Drimys*, *Dussia*, *Erblichia*, *Garrya*, *Gelseminum*, *Heisteria*, *Heliocarpus*, *Hymenaea*, *Louteridium*, *Lunania*, *Lycaste* (*L. skinneri*, monja blanca—the national flower of Guatemala), *Mollinedia*, *Olmediella*, *Oreopanax*, *Rojasianthe*, *Roupala*, *Sloanea*, *Talauma*, *Turpinia*, *Vochysia*.

Deciduous forest association: (temperate upland forest)—*Acer*, *Alnus*, *Berchemia*, *Carpinus*, *Cornus*, *Ilex*, *Juglans*, *Liquidambar*, *Magnolia*, *Ostrya*, *Persea*, *Platanus*, *Prunus*, *Quercus* (oak forests to 3100 m), *Rhus*, *Sambucus*, *Ulmus*.

Coniferous Forest

Gymnosperms: *Abies* (2600–3400 m), *Cupressus*, *Juniperus*, *Pinus* (including highly disturbed pine savannas; *Pinus hartwegii* to timberline), *Taxodium*. Angiosperms: *Acaena*, *Alchemilla*, *Alnus*, *Arbutus*, *Arracacia*, *Buddlei(j)a*, *Fuchsia*, *Holodiscus*, *Lycianthes*, *Oreopanax*, *Oxylobus*, *Pernettya*, *Rubus*, *Werneria*. The pine-oak forest has been severely reduced in extent recently, but potentially it occurs at mid- to lower elevations in the regions mapped as coniferous forest in Fig. 3.84. The three principal vegetation types are juniper-pine (huitales; *Juniperis standleyi–Pinus hartwegii*), fir (*Abies guatemalensis*), and alder-pine forests (*Alnus firmifolia–Pinus hartwegii*).

Alpine Tundra (Páramo)

Agrostis, *Alchemilla*, *Arctostaphylos*, *Arenaria*, *Calamagrostis*, *Draba*, *Festuca*, *Geranium*, *Gnaphalium*, *Haplopappus*, *Lupinus*, *Luzula*, *Muehlenbeckia*, *Potentilla*, *Vaccinium*, *Weldenia*, *Werneria* [above 3300 m in the Cordillera de Cuchumatanes].

APPENDIX 1.11

Plant formations with principal taxa comprising the vegetation of Nicaragua. Species names are provided as a more detailed example of the vegetation of northern Central America because a recent flora with current nomenclature is available (Stevens et al., 2001).

Shrubland/Chaparral–Woodland–Savanna

Bosque seco—Trees: *Astronium graveolens*, *Bursera simaruba*, *Calycophyllum candidissimum*, *Ceiba pentandra*, *Celtis caudata*, *C. iguanaea*, *Gyrocarpus americanus*, *Luehea candida*, *Maclura tinctoria*; shrubs: *Albizia saman*, *Cassia grandis*, *Combretum farinosum*, *Enterolobium cyclocarpum*, *Hymenaea courbaril*; epiphytes: *Brassavola nodosa*, *Tillandsia schiedeana* [mostly on the drier Pacific side, highly disturbed/destroyed from cultivation with only ~1% remaining, 20–25 m in height].

Sabana de pino—Trees, gymnosperms: *Pinus caribea*. Angio-

sperms: *Byrsonima crassifolia*, *Curatella americana*; understory sedges: *Bulbostylis*, *Fimbristylis*, *Rhynchospora*, *Scleria* [mostly on poor soils in wet, inundated regions along the Atlantic coast with MAP of 2500–3500 mm].

Sabana de jícaro (= *Crescentia alata*)—Trees: *Acacia collinsii*, *Byrsonima*, *Caesalpinia coriaria*, *Crescentia alata*, *Pisonia macranthocarpa*; understory grasses: *Aristida ternipes*, *Bouteloua alamosana*, *Oplismenus burmannii*.

Mangrove (Manglares)

Avicennia nitida, *Conocarpus erectus*, *Laguncularia racemosa*, *Rhizophora mangle*.

Beach/Strand/Dune (Playas)

Canavalia rosea, *Ipomoea pes-caprae*, *Sesuvium portulacastrum*; small trees/shrubs: *Hippomane mancinella*, *Sterculia apetala*, *Tamarindus indica*; transition zone behind the playa: *Bromelia pinguin*, *Opuntia guatemalensis*, *Prosopis juliflora*.

Freshwater Herbaceous Bog/Marsh/Swamp

Calathea (several species; e.g., *C. crotalifera*, *C. lutea*, *C. macrosepala*, *C. marantifolia*, *C. micans*), *Heliconia* (several species, e.g., *H. hirsuta*; often in secondary or disturbed vegetation, e.g., *H. collinsiana*, *H. latispatha*, *H. librata*, *H. metallica*), *Pontederia rotundifolia*, *Thalia geniculata*, *Typha domingensis*.

Aquatic

Cabomba haynesii, *Ceratophyllum demersum*, *Echinodorus grandiflorus*, *E. paniculatus*, *Eichornia crassipes*, *Lemna aequinoctialis*, *L. valdiviana*, *Myriophyllum aquaticum*, *Nymphaea ampla*, *N. jamesoniana*, *N. pulchella*, *Nymphoides indica*, *Pistia stratiotes*, *Pontederia rotundifolia*, *Potamogeton pusillus*, *Sagittaria guayanensis*, *S. lancifolia*, *S. longiloba*, *Utricularia* (several species; e.g., *U. erectiflora*, *U. foliosa*, *U. gibba*, *U. hispida*, *U. juncea*, *U. pusilla*, *U. subulata*).

Lowland Neotropical Rain Forest (Pluvioselva)

Andira inermis, *Carapa guianensis*, *Dialium guinense*, *Dipteryx oleifera*, *Laetia procera*, *Tabebuia guayacan*, *Virola koschnyi*, *Vochysia guatemalensis* [eastern part of the Río San Juan region, MAP 4000–6000 mm, elevation ~100–300 m].

Lower to Upper Montane Broad-Leaved Forest

Bosque muy húmedo—*Brosimum alicastrum*, *Cedrela odorata*, *Ceiba pentandra*, *Guarea grandifolia*, *Sciadodendron excelsum*, *Sideroxylon capiri*, *Spondias mombin* [MAP 2000–4000 mm, elevation from sea level to ~800 m].

Bosque nublado o nebliselva (cloud forest association)—Gymnosperms: *Podocarpus oleifolius* (*P. guatemalensis* at lower elevations in the Atlantic zone). Angiosperms: *Alfaroa williamsii*, *Carpinus caroliniana*, *Juglans olanchana*, *Liquidambar styraciflua*, *Matudaea trinervia*, *Oreomunnea mexicana*, *Quercus*, *Symplocos*, *Ulmus mexicana*, South American (Andean) representatives of *Brunellia*, *Gunnera*, and *Weinmannia* [and numerous epiphytes; from 600 m elevation to the elfin forest, ~800 m].

Bosque enano (elfin forest)—*Clusia*, *Hedyosmum*, *Miconia*, *Myrsine*, *Viburnum*.

Pantanos y bosques galería (gallery forest)—*Anacardium excelsum*, *Bactris guineensis*, *Bravaisia integerrima*, *Couroupita nicaraguarensis*, *Erythrina fusca*, *Ficus*, *Heliocarpus appendiculatus*, *Hymenaea courbaril*, *Inga*, *Luehea seemannii*, *Manicaria saccifera*, *Mucuna*, *Ochroma pyramidale*, *Pachira aquatica*, *Pseudobombax septenatum*, *Raphia taedigera*, *Sterculia apetala*, *Symphonia globulifera*.

Coniferous Forest

Bosque de pino y de pino–encino—Gymnosperms: *Pinus maximinoi*, *P. oocarpa*, *P. tecunumanii*. Angiosperms: *Acacia pennatula*, *Arbutus xalapensis*, *Myrica* (*Morella*) *cerifera*, *Quercus* [MAP 1000–2500 mm, elevation below ~650 m], *Tournefortia hirsutissima*, *Trema micrantha*, *Turpinia occidentalis* (to cloud forest), *Weinmannia pinnata*.

APPENDIX 1.12

The plant formations and representative taxa of Costa Rica with the corresponding life zones of Holdridge (1947a).

Desert

None.

Shrubland/Chaparral–Woodland–Savanna (Tropical dry forest)

Ateleia herbert-smithii (illustration, Hartshorn, 1983, p. 128), *Bombacopsis quinata*, *Caesalpinia eriostachys*, *Calycophyllum candidissimum*, *Capparis odoratissima*, *Casearia arguta*, *Chomelia spinosa*, *Croton niveus*, *Enterolobium cyclocarpum*, *Erythroxylum havanense*, *Eugenia salamensis*, *Guazuma ulmifolia*, *Hymenaea courbaril*, *Jacquinia* (*Bonellia*) *pungens*, *Luehea candida*, *Manilkara zapota*, *Piper amalago*, *Pithecellobium saman*, *Tabebuia ochracea* (Hartshorn, 1983, p. 128), *T. rosea*, *Thouinidium decandrum*, *Trichilia americana*, *Zanthoxylum setulosum*.

(Trees found along streams through the tropical dry forest)

Ardisia revoluta, *Brosimum alicastrum*, *Licania arborea*, *Sloanea terniflora*.

(Savanna-like communities)

Byrsonima crassifolia, *Crescentia alata*, *Curatella americana*, *Hyparrhenia rufa* (grass, introduced from Africa), *Trachypogon plumosus* (the characteristic native grass).

(Driest areas [near deserts])

Agave sp., *Bursera permollis*, Cactaceae (*Hylocereus costaricensis*; most cacti [35 species] are epiphytes of the rain forest canopy), *Euphorbia schlechtendalii*, *Guaiacum sanctum* (lignum vitae), *Haematoxylum brasiletto*, *Rehdera trinervis*.

Grassland

None.

Mangrove

[included in the tropical moist forest zone of the Holdridge system]

Avicennia germinans, *Conocarpus erectus*, *Laguncularia racemosa*, *Pelliceria rhizophorae*, *Rhizophora mangle*. Associates: *Acrostichum aureum* (mangrove fern), *Hibiscus tiliaceus*.

Beach/Strand/Dune

Chrysobalanus icaco, *Canavalia maritima* (*C. rosea*), *Enallagma* (*Amphitecna*) *latifolia*, *Hibiscus tiliaceus*, *Hippomane mancinella*, *Ipomoea pes-caprae*.

Freshwater Herbaceous Bog/Marsh/Swamp

Fern: *Blechnum buchtienii*. Angiosperms: *Chusquea tonduzii*, *Escallonia poasana*, *Thalia geniculata*, *Typha domingensis*, *Vaccinium consanguineum*.

Aquatic

Ferns: *Azolla microphylla*, *Ceratopteris thalictroides*, *Salvinia minima*. Angiosperms: *Ceratophyllum muricatum*, *Najas guadalupensis*, *Pistia stratiotes*, *Utricularia foliosa*.

Lowland Neotropical Rain Forest (Tropical wet forest)

None.

Lower to Upper Montane Broad-Leaved Forest

Ferns and allied groups: *Alsophila*, *Cyathea*, *Danaea*, *Lophosoria*, *Lycopodium*, *Pteris*, *Selaginella*. Angiosperms: *Anaxagorea costaricensis*, *Calophyllum longifolium*, *Capparis pittieri*, *Cassipourea elliptica*, *Chrysochlamys* sp., *Dendropanax arboreus*, *Dipteryx oleifera*, *Dussia macroprophyllata*, *Euterpe precatoria*, *Faramea suerrensis*, *Goethalsia meiantha*, *Guarea rhopalocarpa*, *Hernandia didymantha*, *Inga thibaudiana*, *Laetia procera*, *Macrocnemum roseum*, *Perebea angustifolia*, *Protium pittieri*, *Qualea paraensis*, *Quararibea bracteolosa*, *Rinorea squamata*, *Ryania speciosa*, *Swartzia simplex*, *Symphonia globulifera*, *Tetragastris panamensis*, *Trophis involucrata*, *Vantanea barbourii*, *Vochysia ferruginea*, *Warszewiczia coccinea*.

Cloud forest association (in the path of the northeast trade winds, trunks covered with mosses and other epiphytes, e.g., *Begonia estrellensis*, *Hydrangea peruviana*): *Alchornea latifolia*, *Alfaroa costaricensis*, *Allophylus racemosus*, *Alnus acuminata*, *Ardisia palmana*, *Bursera grandifolia*, *Calocarpum viride*, *Casearia aculeata*, *Casimiroa edulis*, *Cedrela odorata*, *Celtis iguanaea*, *Citharexylum macradenium*, *Cornus disciflora*, *Cosmibuena grandiflora*, *Cupania glabra*, *Daphnopsis americana*, *Dendropanax gonatopodus*, *Diospyros* sp., *Eugenia* sp., *Faramea capulifolia*, the strangler figs *Ficus crassiuscula* and *F. tuerckheimii*, *Guarea tuisana* (= *G. rhopalocarpa*), *Guatteria consanguinea*, *Hampea appendiculata*, *Hauya lucida*, *Hibiscus acetosella*, *Hiraea haberi*, *Magnolia poasana*, *Meliosma vernicosa*, *Mimosa albida*, *Morella* sp., *Mortoniodendron anisophyllum*, *Oreomunnea pterocarpa*, *Oreopanax xalapensis*, *Sabicea panamensis*, *Sapium glandulosum*, *S. pachystachys*, *Sloanea medusula*, *Styphnolobium monteviridis*, *Weinmannia wercklei*.

Elfin forest association: *Chrysochlamys*, *Quercus corrugata*, *Q. seemannii* with *Billia hippocastanum*, *Brunellia costaricensis*, *Buddleja nitida*, *Clethra gelida*, *Comarostaphylis arbutoides*, *Ficus crassiuscula*, *Hieronyma oblonga*, *Oreopanax nubigenus*, *O. xalapensis*, *Persea americana*, *P. schiedeana*, *Rhamnus oreodendron*, *Schefflera rodriguesiana*, *Tovomita*, *Viburnum costaricanum*, *Weinmannia pinnata*, *W. wercklei*, *Zanthoxylum melanostictum*.

Near contact with the páramo: dwarf oaks often dominant, with shrubs of Ericaceae (e.g., *Vaccinium consanguineum*), *Didymopanax pittieri* (*Schefflera rodriguesiana*), *Miconia biperulifera*, *Morella cerifera*, *Weinmannia pinnata*.

Alpine Tundra

(Páramo, subalpine rain páramo; ~3100–3500 m)

Fern: *Jamesonia* sp. Angiosperms: numerous Gramineae (*Chusquea*, a bamboo), *Gunnera talamancana*, *Hypericum irazuense*, *Vaccinium consanguineum*, *Viburnum costaricanum*, bog plants (*Cirsium* sp., *Puya dasylirioides*).

Seral and Disturbed Vegetation

Castilla elastica, *Cecropia peltata*, *Cochlospermum vitifolium*, *Guazuma ulmifolia*, *Muntingia calabura*.

APPENDIX 1.13

Representative taxa of the lowland Neotropical rain forest and associations in Costa Rica (Hartshorn, 1983, and other sources).

Prominent Trees of the Lowland Neotropical Rain Forest

Ardisia cutteri, *Aspidosperma megalocarpon*, dwarf palms (*Asterogyne martiana*, *Calyptrogyne sarapiquensis*, *Geonoma congesta*, *Iriartea gigantea*, *Socratea durissima*, *Synechanthus warscewiczianus*, *Welfia georgii*), *Brosimum alicastrum*, *B. guianens*, *B. utile*, *Caryocar costaricense*, *Garcia nutans*, *Hura crepitans*, *Scheelea* (*Attalea*) *rostrata*, *Licania arborea*, *Manilkara zapota* (chicle), *Peltogyne purpurea*, *Pentaclethra macroloba*, *Protium copal*, *Sapindus saponaria*, *Sorocea pubivena*, *Symphonia globulifera*, *Talisia nervosa*, *Terminalia oblonga*,

Trophis racemosa, *Virola* sp., *Vochysia* sp.

Associations that Include Forests on the Raised Parts of the Swamp

Gymnosperm: *Podocarpus oleifolius*. Angiosperms: *Adelia triloba*, *Alchornea latifolia*, *Andira inermis*, *Astrocaryum alatum*, *Bactris longiseta*, *Carapa guianensis*, *Clusia alata*, *Conostegia* sp., *Crateva tapia*, *Cryosophila guagara*, *Dendropanax arboreus*, *D. gonatopodus*, *Dialyanthera otoba*, *Erythrina lanceolata*, *Grias fendleri*, *Guatteria consanguinea*, *Hieronyma poasana*, *Inga vera*, *Ipomoea* sp., *Luehea seemanii*, *Magnolia* sp., *Mouriri* sp., *Parkinsonia aculeata* (palo verde), *Persea schiedeana*, *Piper cenocladum*, *Prestoea decurrens*, *Pterocarpus officinalis* (Hartshorn, 1983, p. 118), *Quercus corrugata*, *Q. seemannii*, *Raphia taedigera* (yolillo palm), *Sapium pachystachys*, *Tetrorchidium* sp., *Tovomita nicaraguensis*, *Virola koschnyi*, *Weinmannia wercklei*.

Frequently Inundated River Floodplain Forests and Recent Alluvial Terraces

Alchornea costaricensis, *Anacardium excelsum*, *Basiloxylon excelsum*, *Bravaisia integerrima*, *Bursera simaruba*, *Caryocar costaricense*, *Castilla elastica*, *Ceiba pentandra* (the tallest tree in Central America, to >40 m tall; Fig. 3.117), *Chamaedorea exorrhiza*, *Cordia alliodora*, *Croton schiedeanus*, *Erythrina cochleata*, *Ficus tonduzii*, *Hernandia didymantha*, *H. stenura*, *Hura crepitans*, *Inga densiflora*, *I. oerstediana*, *Lonchocarpus oliganthus*, *Mora oleifera*, *Pithecellobium longifolium*, *Prioria copaifera*, *Spondias radlkoferi*, *Terminalia oblonga*, *Trophis racemosa*, *Zanthoxylum panamense*.

Swamp Forest Associations Near Dry Dune Areas

Caesalpinia coriaria, *Prosopis juliflora*.

APPENDIX 1.14

Principal tree species in the life zones of the Monteverde region (montane broad-leaved forest), Costa Rica (from Haber, 2000).

Lower to Upper Montane Broad-Leaved Forest

Tropical moist forest

Anacardium excelsum, *Ardisia revoluta*, *Astronium graveolens*, *Beilschmiedia* sp., *Bombacopsis quinatum*, *Brosimum alicastrum*, *Capparis cynophallophora*, *Cecropia obtusifolia*, *C. peltata*, *Cedrela salvadorensis*, *Ceiba aesculifolia*, *Clarisia biflora*, *Croton draco*, *Cupania guatemalensis*, *Erblichia odorata*, *Eugenia salamensis*, *Ficus citrifolia*, *F. trachelosyce*, *F. yoponensis*, *Hura crepitans*, *Lonchocarpus haberi*, *Nectandra martinicensis*, *Ochroma pyramidale*, *Ocotea veraguensis*, *Picramnia antidesma*, *Sideroxylon capiri*, *Terminalia oblonga*, *Thouinidium decandrum*, *Trichilia glabra*, *T. martiana*, *Triplaris melaenodendron*.

Premontane moist forest

Agonandra macrocarpa, *Albizia adinocephala*, *Beilschmiedia* sp., *Bravaisia integerrima*, *Bursera simaruba*, *Byrsonima crassifolia*, *Casimiroa edulis*, *Chrysophyllum brenesii*, *Cinnamomum brenesii*, *Clarisia biflora*, *Clethra lanata*, *Cordia stellifera*, *Cupania guatemalensis*, *Dilodendron costaricense*, *Diphysa americana*, *Drypetes laterifolia*, *Ficus laterisyce*, *Ilex haberi*, *Licaria triandra*, *Lonchocarpus oliganthus*, *Luehea speciosa*, *Manilkara chicle*, *Myrcianthes* sp., *Nectandra salicina*, *Ocotea sinuata*, *Psidium sartorianum*, *Roupala montana*, *Sapium macrocarpum*, *Sideroxylon persimile*, *Styrax argenteus*, *Zanthoxylum monophyllum*.

Premontane wet forest

Beilschmiedia brenesii, *Billia columbiana*, *Cecropia obtusifolia*, *Cedrela tonduzii*, *Chionanthus panamensis*, *Cinnamomum cinnamomifolium*, *Citharexylum integerrimum*, *Conostegia xalapensis*, *Croton mexicanus*, *Dendropanax arboreus*, *Eugenia monticola*, *Exothea paniculata*, *Ficus tuerckheimii*, *Gymnosporia haberiana*, *Inga sierrae*, *Matayba oppositifolia*, *Meliosma idiopoda*, *Mortoniodendron costaricense*, *Nectandra membranacea*, *Ocotea monteverdensis*, *O. whitei*, *Pouteria exfoliata*, *Randia matudae*, *Roupala glaberrima*, *Sapium laurifolium*, *Sideroxylon stenospermum*, *Stauranthus perforatus*, *Styphnolobium monteviridis*, *Symplocos limoncillo*.

Lower montane wet forest

Ardisia palmata, *Beilschmiedia costaricensis*, *Casearia tacanensis*, *Chione sylvicola*, *Citharexylum caudatum*, *Cojoba costaricensis*, *Conostegia oerstediana*, *C. pittieri*, *Dendropanax querceti*, *Dussia* sp., *Eugenia guatemalensis*, *E. octopleura*, *Guarea tonduzii*, *Hasseltia floribunda*, *Inga micheliana*, *Matayba* sp., *Maytenus recondita*, *Meliosma vernicosa*, *Mortoniodendron costaricense*, *Myrcianthes fragrans*, *Ocotea insularis*, *O. meziana*, *Persea americana*, *Pleurothyrium palmanum*, *Pouteria fossicola*, *Quararibea costaricensis*, *Sapium glandulosum*, *Sloanea ampla*, *Symplocos brenesii*, *Weinmannia wercklei*.

Lower montane rain forest

Gymnosperm: *Podocarpus monteverdeensis*. Angiosperms: *Alchornea latifolia*, *Ardisia solomonii*, *Billia hippocastanum*, *Brunellia costaricensis*, *Calyptranthes monteverdensis*, *Cecropia polyphlebia*, *Conostegia rufescens*, *Dendropanax latilobus*, *Elaeagia auriculata*, *Eugenia valerioi*, *Ficus crassiuscula*, *Guarea kunthiana*, *Guettarda poasana*, *Ilex costaricensis*, *Inga longispica*, *Magnolia poasana*, *Ocotea* cf. *virdiflora*, *O.* near *O. insularis*, *Persea schiedeana*, *Prestoea acuminata*, *Prunus brachybotrya*, *Quercus corrugata*, *Ruagea glabra*, *Salacia petenensis*, *Sapium rigidifolium*, *Symplocos povedae*, *Tovomitopsis allenii*, *Viburnum venustum*, *Weinmannia pinnata*, *Zanthoxylum melanostictum*.

Premontane rain forest

Allophylus psilospermus, *Bourreria costaricensis*, *Capparis discolor*, *Cecropia insignis*, *Cedrela tonduzii*, *Chrysophyllum hirsutum*, *Citharexylum donnell-smithii*, *Cupania* sp., *Elaeagia uxpanapensis*, *Guarea kunthiana*, *Inga leonis*, *Lunania mexicana*, *Meliosma vernicosa*, *Mortoniodendron anisophyllum*, *Naucleopsis capirensis*, *Ocotea meziana*, *Pleurothyrium palmanum*, *Pouteria austin-smithii*, *Pseudolmedia mollis*,

Psychotria eurycarpa, *Pterocarpus* cf. *rohrii*, *Quararibea costaricensis*, *Rauvolfia aphlebia*, *Sapium laurifolium*, *S. rigidifolium*, *Ticodendron incognitum*, *Trichilia martiana*, *Trophis mexicana*.

Tropical wet forest/transition

Acacia ruddiae, *Albizia carbonaria*, *Alchornea costaricensis*, *A. glandulosa*, *Calatola costaricensis*, *Cespedesia macrophylla*, *Chimarrhis parviflora*, *Chionanthus oblanceolatus*, *Chomelia venulosa*, *Croton megistocarpus*, *Dussia* sp., *Ficus crassivenosa*, *Hedyosmum bonplandianum*, *Inga barbourii*, *Iriartea deltoidea*, *Jacaratia spinosa*, *Mortoniodendron anisophyllum*, *Ocotea dentata*, *O. stenoneura*, *Oreomunnea pterocarpa*, *Otoba novogranatensis*, *Pachira aquatica*, *Pentagonia costaricensis*, *Platymiscium* sp., *Pouteria congestifolia*, *Sapium rigidifolium*, *Sloanea ligulata*, *Terminalia bucidoides*, *Theobroma mammosum*, *Vochysia guatemalensis*, *Zinowiewia costaricensis*.

APPENDIX 1.15

Representative taxa of the plant formations of Panama correlated with the life zones of Holdridge and Budowski (1956). Based on Porter (1973; swamp vegetation based on Phillips et al., 1997).

Desert

None.

Shrubland/Chaparral–Woodland–Savanna

(Tropical dry forest/transition)

Acacia costaricensis, *A. farnesiana*, *Agave panamana*, *Bombacopsis quinata*, *Bursera simaruba*, *Byrsonima crassifolia*, Cactaceae (cacti; *Acanthocereus pentagonus*, *Hylocereus polyrhizus*, *Opuntia elatior*), *Caesalpinia crista*, *Calea prunifolia*, *Celtis iguanaea*, *Cochlospermum vitifolium*, *Curatella americana*, *Erythroxylum mexicanum*, Gramineae (grasses; *Andropogon angustatus*, *A. brevifolius*, *Panicum molle*, *Setaria tenax*), *Guettarda odorata*, *Hippomane mancinella*, *Pisonia aculeata*, *Plumeria rubra*, *Prosopis juliflora*.

Grassland

None.

Mangrove

Ferns and allied groups: *Acrostichum aureum*, *Cyclopeltis semicordata*. Angiosperms: *Avicennia bicolor*, *A. germinans*, *Conocarpus erectus*, *Dieffenbachia longispatha*, *Hibiscus tiliaceus*, *Laguncularia racemosa*, *Pelliciera rhizophorae*, *Raphia taedigera*, *Rhizophora mangle*, *Rhynchospora macrostachya*, *Sagittaria lancifolia*.

Associated trees/shrubs: *Cassipourea elliptica*, *Chrysobalanus icaco*, *Citharexylum caudatum*, *Clusia*, *Enallagma latifolia*, *Euterpe precatoria*, *Mora oleifera*, *Pithecellobium*, *Plumeria rubra*, *Tabebuia palustris*, *Tecoma stans*, *Xylosma panamensis*.

Beach/Strand/Dune

Dalbergia brownei, *Hippomane mancinella*, *Ipomoea pes-caprae*, *Tecoma stans*, *Uniola pittieri*.

Freshwater Herbaceous Bog/Marsh/Swamp

Trees, shrubs, large herbs: *Alchornea*, *Bactris major*, *Browneopsis excelsa*, *Campnosperma panamensis*, *Carapa guianensis*, *Cassia reticulata*, *Cespedezia macrophylla*, *Copaifera aromatica*, *C. panamensis*, *Cyrilla racemifolia*, *Erythrina glauca*, *Manicaria saccifera*, *Miconia curvipetiolata*, *Mortoniodendron*, *Myrica mexicana*, *Neea*, *Ouratea*, *Pachira aquatica*, *Posoqueria latifolia*, *Prioria copaifera*, *Protium panamensis*, *Pterocarpus officinalis*, *Quararibea asterolepis*, *Q. bracteolosa*, *Q. pterocalyx*, *Raphia taedigera*, *Symphonia globulifera*, *Tabebuia pentaphylla*.

Herbaceous—Bryophyte: *Sphagnum*. Angiosperms: Cyperaceae, *Drosera*, Gramineae, *Pontederia cordata*, *Sagittaria lancifolia*, *Thalia* sp., *Typha angustifolia*, *Utricularia mixta*.

Aquatic

Ferns: *Ceratopteris* sp., *Marsilea* sp., *Salvinia auriculata*. Angiosperms: *Eichornia azurea*, *Lemna cyclostasa*, *Nymphaea ampla*, *Nymphoides humboldtiana*, *Pistia stratioites*, *Utricularia* sp.

Lowland Neotropical Rain Forest

Allophylus occidentalis, *Alseis blackiana*, *Amaioua corymbosa*, *Anacardium excelsum*, *Andira inermis*, *Astrocaryum standleyanum*, *Bombacopsis quinata*, *B. sessilis*, *Calycophyllum candidissimum*, *Cavanillesia platanifolia*, *Cedrela odorata*, *Ceiba pentandra*, *Chamaedorea wendlandiana*, *Chione chambersii*, *Chomelia recordii*, *Enterolobium cyclocarpum*, *Ficus nymphaeifolia*, *Guarea guidonia*, *Gustavia nana*, *Hirtella racemosa*, *Hura crepitans*, *Licania hypoleuca*, *Luehea seemanii*, *Mabea occidentalis*, *Miconia argentea*, *Mouriri parvifolia*, *Myrcia splendens*, *Neea amplifolia*, *Ouratea lucens*, *Pera arborea*, *Pithecellobium rufescens*, *Platypodium elegans*, *Posoqueria latifolia*, *Protium panamense*, *Pseudobombax septenatum*, *Quararibea asterolepis*, *Q. bracteolosa*, *Randia armata*, *Scheelea zonensis*, *Spondias mombin*, *Stemmadenia grandiflora*, *Sterculia apetala*, *Swartzia simplex*, *Swietenia macrophylla*, *Terminalia amazonica*, *Tetragrastris panamensis*, *Trophis racemosa*, *Vitex cymosa*, *V. masoniana*, *Xylopia aromatica*, *Zanthoxylum panamense*.

Lower to Upper Montane Broad-Leaved Forest

(Tropical moist forest/transition, subtropical moist forest, subtropical dry forest, lower montane wet forest, montane wet forest)

Gymnosperm: *Podocarpus guatemalensis*. Angiosperms: *Acacia riparia*, *Alfaroa costaricensis*, *Brosimum guianense*, *Brownea macrophylla*, *Brunellia costaricensis*, *Byrsonima dressleri*, *Calophyllum brasiliense*, *Cedrela tonduzii*, *Chomelia spinosa*, *Conostegia xalapensis*, *Faramea jefensis*, *Hampea micrantha*, *Hoffmannia capillacea*, *Ilex guianensis*, *Lisianthius jefensis*, *Oenocarpus panamanus*, *Pentagonia macrophylla*, *Persea schiedeana*, *Posoqueria latifolia*, *Psychotria grandicarpa*,

Quararibea dolichopoda, *Quercus copeyensis*, *Rondeletia salicifolia*, *Siparuna pauciflora*, *Stemmadenia grandiflora*, *Ternstroemia tepezapote*, *Vochysia jefensis*, *Warszewiczia coccinea*, *Weinmannia pinnata*, *Xylopia frutescens*.

Additional genera (most common taxa) from old-growth forest, Barro Colorado Island (Hubbell & Foster, 1990): *Acalypha diversifolia*, *Beilschmiedia pendula*, *Capparis frondosa*, *Cordia lasiocalyx*, *Coussarea curvigemmia*, *Cupania sylvatica*, *Desmopsis panamensis*, *Drypetes standleyi*, *Eugenia galalonensis*, *Hasseltia floribunda*, *Hybanthus prunifolius*, *Lacistema aggregatum*, *Maquira costaricana*, *Mouriri myrtilloides*, *Ocotea skutchii*, *Piper cordulatum*, *Poulsenia armata*, *Pouteria unilocularis*, *Rheedia edulis*, *Rinorea sylvatica*, *Simarouba amara*, *Sorocea affinis*, *Tabernaemontana arborea*, *Tachigalia versicolor*, *Trichilia tuberculata*, *Virola sebifera*.

APPENDIX 1.16

Summary of the principal genera mentioned in the text that characterize the plant communities of Central America, including the representation of the genera and communities in the microfossil record. An asterisk (*) indicates the genus has been identified from the Cenozoic of Central America. A double asterisk (**) indicates the fossil can be referred only to a broader taxonomic category (e.g., group of genera, family or group of families).

Shrubland/Chaparral–Woodland–Savanna

**Acacia*, *Acanthocereus*, *Achras*, *Agave*, *Albizia*, *Andropogon*, *Aristida*, *Astronium*, *Ateleia*, *Bacopa*, *Bombacopsis*, *Bouteloua*, *Brassavola*, *Brosimum*, **Bursera*, *Byrsonima*, **Caesalpinia*, *Calea*, *Calophyllum*, *Capparis*, **Casearia*, *Cassia*, *Ceiba* (disturbed habitats), *Celtis*, *Cephalocereus*, *Chomelia*, *Cochlospermum*, ***Combretum*, *Conobea*, *Crescentia*, *Croton*, *Crumenaria*, **Cryosophila*, *Curatella*, *Diodia*, *Echinodorus*, *Enterolobium*, *Erythroxylum*, ***Eugenia*, *Euphorbia*, *Evolvulus*, **Ficus*, *Fimbristylis*, *Gliricidia*, *Gomphrena*, **Gramineae, *Guaiacum*, **Guazuma*, *Guettarda*, *Gyrocarpus*, *Haematoxylum*, *Hippomane*, *Hylocereus*, *Hymenaea*, *Jacquinia*, *Juliania*, *Karwinskia*, *Lemaierocereus*, *Limnobium*, *Lucuma*, *Luehea*, *Maclura*, *Manilkara*, *Opuntia*, *Pacourina*, *Panicum*, *Pereskia*, *Phorodendron*, *Piper*, *Pisonia*, *Pithecellobium*, *Plumeria*, *Portulaca*, *Prosopis*, *Psychotria*, *Rehdera*, *Rheedia*, *Ruprechtia*, *Scleria*, *Setaria*, *Sida*, *Sterculia*, *Swietenia*, *Tabebuia*, *Talinum*, *Thouinidium*, **Tillandsia*, *Trichilia*, *Zanthoxylum*.

Mangrove

Principal genera: *Avicennia*, *Conocarpus*, *Laguncularia*, **Pelliceria*, **Rhizophora*; associate genera—Fern: ***Acrostichum*. Angiosperms: *Chrysobalanus*, *Citharexylum*, *Enallagma*, **Hibiscus*, *Mora*, *Plumeria*, *Tabebuia*, *Tecoma*, *Xylosma*.

Beach/Strand/Dune

Bromelia, *Canavalia*, *Chrysobalanus*, *Dalbergia*, *Enallagma*, **Gramineae, *Hippomane*, *Ipomoea*, *Opuntia*, *Prosopis*, *Sesuvium*, *Sterculia*, *Tamarindus*, *Tecoma*, *Uniola*.

Freshwater Herbaceous Bog/Marsh/Swamp

Ferns and allied groups: ***Acrostichum*, *Blechnum*, *Dryopteris*, *Nephrolepis*. Angiosperms: *Bactris*, *Browneopsis*, *Calathea*, **Campnosperma*, *Carapa*, *Cassia*, *Copaifera*, **Cyperaceae (*Cyperus*, *Eleocharis*, *Fuirena*, *Scleria*), **Erythrina*, *Escallonia*, **Gramineae (*Andropogon*, *Chusquea*, *Phragmites*), *Heliconia*, **Ludwigia*, **Manicaria*, *Pachira*, **Palmae, *Polygonum*, *Pontederia*, *Posoqueria*, *Prioria*, *Pterocarpus*, *Quararibea*, *Raphia*, *Sagittaria*, **Symphonia*, *Tabebuia*, *Thalia*, *Typha*, *Vaccinium* (**Ericaceae).

Aquatic

Ferns and allied groups: **Ceratopteris*, *Marsilea*, *Salvinia*. Angiosperms: **Cabomba*, *Ceratophyllum*, *Echinodorus*, *Eichhornia*, *Lemna*, *Myriophyllum*, *Najas*, *Nymphaea*, *Nymphoides*, *Pennisetum*, *Pistia*, *Pontederia*, *Potamogeton*, *Sagittaria*, **Utricularia*.

Lowland Neotropical Rain Forest

**Allophylus*, *Alseis*, *Amaioua*, *Anacardium*, *Andira*, *Ardisia*, *Aspidosperma*, *Asterogyne*, *Astrocaryum*, *Bauhinia*, **Bernoulia* (to lower montane), *Calocarpum*, *Calycophyllum*, *Calyptrogenia*, *Calyptrogyne*, *Carapa*, *Cavanillesia*, *Chamaedorea*, *Chione*, **Chrysophyllum*, **Crudia*, **Cryosophila*, **Cymbopetalum*, *Dialium*, *Dipteryx*, *Entada*, *Enterolobium*, *Ficus*, *Geonoma*, **Gramineae, *Gustavia*, *Hexopetion*, *Hirtella*, *Iriartea*, **Lacmellea*, *Laetia*, *Licania*, *Mabea*, *Manilkara*, **Mortoniodendron*, *Neea*, *Orbignya*, *Ouratea*, **Palmae, **Paullinia*, *Peltogyne*, *Pentaclethra*, *Pera*, *Platypodium*, *Posoqueria*, **Protium*, *Sapindus*, *Scheelea*, *Sorocea*, *Stemmadenia*, *Swietenia*, **Symphonia*, *Tabebuia*, *Talisia*, ***Terminalia*, *Trophis*, *Virola*, *Vochysia*.

Lower to Upper Montane Broad-Leaved Forest

Ferns and allied groups: *Acrostichum*, **Alsophila*, **Cnemidaria*, **Ctenitis*, **Cyathea*, **Dannea*, **Grammitis*, **Lophosoria*, **Lycopodium*, **Ophioglossum*, **Pityrogramma*, **Pteris*, **Selaginella*. Gymnosperms: *Ceratozamia*, **Podocarpus*, *Taxus*. Angiosperms: **Acacia*, *Adelia*, **Aegiphila* (to moist), *Agonandra*, *Albizia*, **Alchornea*, **Alfaroa–Oreomunnea*, **Allophylus*, *Anacardium*, *Anaxagorea*, *Ardisia*, *Astronium*, *Bactris*, *Basiloxylon*, *Begonia*, *Beilschmiedia*, *Berchemia*, *Billia*, *Bombacopsis*, *Bourreria*, *Bravaisia*, *Brosimum*, *Brownea*, **Brunellia*, *Buddleja*, **Bursera*, *Byrsonima*, **Caesalpinia*, *Calatola*, *Calocarpum*, *Calophyllum*, *Calyptranthes*, *Capparis*, **Cardiospermum* (widespread), *Cariniana*, *Caryocar*, **Casearea*, **Casimiroa*, *Cassipourea*, *Castilla*, **Cedrela*, *Ceiba*, *Cespedesia*, *Cestrum*, *Chamaedorea*, *Cheiranthodendron*, *Chimarrhis*, *Chionanthus*, *Chione*, *Chomelia* (fossil as *Chomelia* type), *Chrysochlamys*, **Chrysophyllum*, *Cinnamomum*, *Citharexylum*, *Clarisia*, *Clethra*, *Clusia*, **Coccoloba*

(moist, including coastal), *Cojoba*, *Comarostaphylis*, **Combretum–Terminalia* (moist, some species into drier to more humid habitats), *Conostegia*, *Cordia*, **Cosmibuena*, *Couroupita*, *Crateva*, *Croton*, **Cupania*, **Cyperaceae, *Dahlia*, *Daphnopsis*, *Dendropanax*, *Dialyanthera*, *Didymopanax*, *Dilodendron*, *Diphysa*, *Dipteryx*, **Doliocarpus*, *Drimys*, *Drypetes*, *Dussia*, *Elaeagia*, *Erblichia*, **Erythrina*, ***Eugenia*, *Euterpe*, *Exothea*, **Faramea*, **Ficus*, *Garrya*, *Gelseminum*, *Goethalsia*, **Gramineae, *Grias*, **Guarea*, *Guatteria*, *Guettarda*, *Gunnera*, *Gymnosporia*, ***Hampea*, *Hasseltia*, **Hauya*, *Hedyosmum*, *Heisteria*, *Heliocarpus*, *Hernandia*, ***Hibiscus*, *Hieronyma*, *Hiraea*, *Hoffmannia*, *Hura*, *Hydrangea*, *Hymenaea*, **Ilex*, *Inga*, *Iriartea*, *Jacaratia*, *Laetia*, *Licania*, *Licaria*, **Lisianthius*, *Lonchocarpus*, *Louteridium*, **Ludwigia*, *Luehea*, *Lunania*, *Lycaste*, *Macrocnemum*, **Manicaria*, *Manilkara*, **Matayba*, *Maytenus*, *Meliosma*, *Miconia*, *Mimosa*, *Mollinedia*, *Mora*, *Mouriri*, *Mucuna*, *Myrcianthes*, *Myrsine*, *Naucleopsis*, *Nectandra*, *Ochroma*, *Ocotea*, *Oenocarpus*, *Olmediella*, *Oreopanax*, *Otoba*, *Ouratea*, **Palmae, *Parkinsonia*, *Pentagonia*, *Perebea*, *Persea*, **Petrea*, *Picramnia*, *Piper*, *Pithecellobium*, *Platymiscium*, *Pleurothyrium*, **Posoqueria* (to more moist, dry), **Pouteria*, *Prestoea*, *Prioria*, *Protium*, **Pseudobombax*, *Pseudolmedia*, *Psidium*, *Psychotria*, *Pterocarpus*, *Quararibea*, *Randia*, *Raphia*, *Rauvolfia*, *Rinorea*, *Rojasianthe*, *Rondeletia*, *Roupala*, *Ruagea*, *Ryania*, **Sabicea*, *Salacia*, **Sapium*, *Schefflera*, *Sciadodendron*, **Serjania*, *Sideroxylon*, *Siparuna*, *Sloanea*, *Spondias*, *Stauranthus*, *Stemmadenia*, *Sterculia*, *Styphnolobium*, *Styrax*, *Swartzia*, **Symphonia*, **Symplocos*, *Talauma*, ***Terminalia*, *Ternstroemia*, **Tetragrastis*, **Tetrorchidium*, *Theobroma*, *Thouinidium*, *Ticodendron*, *Tovomita*, *Tovomitopsis*, *Trichilia*, *Triplaris*, *Trophis*, *Turpinia*, *Vantanea*, *Viburnum*, *Virola*, *Vitex*, *Vochysia*, *Warszewiczia*, *Weinmannia*, *Xylopia*, *Zanthoxylum*, *Zinowiewia*. Deciduous forest association: *Acer*, **Alfaroa–Oreomunnea* (*Engelhardia*), *Alnus*, *Berchemia*, *Carpinus*, **Carya* (Plio–Pleistocene, El Salvador), *Celtis*, *Cornus*, *Diospyros*, **Ilex*, **Juglans*, *Liquidambar*, *Magnolia*, *Matudaea*, **Mortoniodendron*, *Myrica*, *Ostrya*, *Persea*, *Platanus*, *Prunus*, **Quercus*, *Rhamnus*, *Rhus*, *Sambucus*, **Symplocos*, **Ulmus*.

Coniferous Forest

Gymnosperms: *Abies*, *Cupressus*, *Juniperus*, **Picea* (Mio–Pliocene, Guatemala; now south only to northern Mexico), **Pinus*, *Taxodium*. Angiosperms: **Acacia*, *Acaena*, *Alchemilla*, *Alnus*, *Arbutus*, *Arracacia*, *Buddlei(j)a*, *Fuchsia*, *Holodiscus*, *Lycianthes*, *Myrica*, *Oreopanax*, *Oxylobus*, *Pernettya*, **Quercus*, *Rubus*, *Werneria*.

Alpine Tundra (Páramo)

Fern: *Jamesonia*. Angiosperms: *Agrostis*, *Alchemilla*, *Arctostaphylos*, *Arenaria*, *Calamagrostis*, *Chusquea*, *Cirsium*, *Draba*, *Festuca*, *Geranium*, *Gnaphalium*, *Gunnera*, *Haplopappus*, *Hypericum*, *Lupinus*, *Luzula*, *Muehlenbeckia*, *Potentilla*, *Puya*, *Vaccinium*, *Viburnum*, *Weldenia*, *Werneria*.

APPENDIX 1.17

Plant formations and representative species in the vegetation of Venezuela (based on Ewel et al., 1976). Numbers refer to vegetation types on Fig. 3.127. Names in parentheses are those used by Ewel et al. (1976).

1. Desert

(Maleza desértica tropical)

Cercidium praecox, *Jacquinia aciculata*, *Lemaireocereus griseus*, *Mammillaria* sp., *Opuntia caracassana*, *Poponax* sp., *Prosopis juliflora*.

2, 3, 4, 7, 8. Shrubland/Chaparral–Woodland–Savanna

(Monte espinosa tropical, bosque muy seco tropical, bosque seco tropical, monte espinoso premontano, bosque seco premontano)

Acacia macracantha, *A. tortuosa*, *Acnistus ramiflorus*, *Acrocomia sclerocarpa* (*Cocos aculeatus*), *Agave* sp., *Anacardium excelsum*, *Andira inermis*, *Apeiba tibourbou*, *Aristida venezuelae*, *Astronium graveolens*, *Attalea* sp., *Banisteria argentea*, *Bauhinia* sp., *Beureria* (*Bourreria*) *cumanensis*, *Bombacopsis quinata*, *Bombax* sp., *Bowdichia virgilioides*, *Bromelia humilis*, *Brownea aroensis*, *Bulnesia arborea*, *Bumelia buxifolia*, *Bursera simaruba*, *B. tomentosa*, *Byrsonima crassifolia*, *Caesalpinia coriaria*, *C. granadillo*, *Calliandra purpurea*, *Calycophyllum candidissimum*, *Capparis flexuosa*, *C. linearis*, *C. odoratissima*, *C. tenuisiliqua*, *Casearia guianensis*, *Cassia emarginata*, *C. grandis*, *C. moschata*, *C. obovata*, *C. reticulata*, *Castela nicholsoni*, *Cecropia peltata*, *Cedrela mexicana*, *Ceiba pentandra* (relict), *Cephalocereus moritzianus*, *Cercidium praecox*, *Cereus deficiens*, *C. griseus*, *C. margaritensis*, *Chlorophora tinctoria*, *Chrysobalanus icaco*, *Citharexylum* sp., *Coccoloba caracasana*, *C. coronata*, *Cochlospermum vitifolium*, *Copaifera officinalis*, *C. pubiflora*, *Copernicia tectorum*, *Cordia alba*, *C. alliodora*, *C. globosa*, *Couroupita guianensis*, *Crateva* sp., *Crescentia cujete*, *Croton bredemeyeri*, *C. ovalifolius*, *C. punctatum*, *C. rhamnifolioides*, *Curatella americana*, *Datura stramonium*, *Didymopanax morototoni*, *Dodonaea viscosa*, *Duranta repens*, *Enterolobium cyclocarpum*, *Erythrina glauca*, *Genipa caruto*, *Gliricidia sepium*, *Guaiacum officinale*, *Guarea trichilioides* (*G. grandiflora*), *Guazuma ulmifolia*, *Hura crepitans*, *Hymenaea courbaril*, *Hyptis* sp., *Jacquinia aciculata*, *J. barbasco*, *Jatropha gossypiifolia*, *J. urens*, *Lantana moritziana*, *Lemaireocereus griseus*, *Libidibia granadillo*, *Lippia alba*, *L. origanoides*, *Lonchocarpus* sp., *Luehea candida*, *Lycium tweedianum*, *Malpighia glabra*, *Mammillaria mammillaria*, *Mauritia minor*, *Melicocca* (*Melicoccus*) *bijugatus*, *Melocactus caesius*, *Mimosa arenosa*, *M. tenuiflora*, *Morisonia americana*, *Muntingia calabura*, *Ochroma lagopus*, *Opuntia caracassana*, *O. caribaea*, *Parkinsonia aculeata*, *Pectis linifolia*, *Pereskia guamacho*, *Persea caerulea*, *Petrea arborea*, *Phyllanthus botryanthus*, *Pilocarpus alvaradoi*, *Pithecellobium falconiense*, *P. hymenaeifolium*, *P. saman*, *Platymiscium pinnatum*, *P. polystachyum*, *Poponax farnesiana*, *Pouteria carabobensis*, *Prosopis*

juliflora, *Pterocarpus podocarpus*, *Roupala complicata*, *Roystonea* sp., *Ruprechtia ramiflora*, *Sapindus saponaria*, *Solanum argillicolum*, *Spondias mombin*, *Sterculia apetala*, *Swietenia macrophylla*, *Tabebuia billbergii*, *T. chrysantha*, *T. pentaphylla*, *T. serratifolia*, *Talisia oliviformis*, *Tamarindus indica*, *Tecoma stans*, *Tetrapterys* sp., *Trachypogon* sp., *Trema micrantha*, *Triplaris caracasana*, *Vochysia* sp., *Wigandia caracasana*.

5, 6. Lowland Neotropical Rain Forest

(Bosque húmedo tropical, bosque muy húmedo tropical)

Alexa imperatricis, *Anacardium excelsum*, *Apeiba tibourbou*, *Astronium graveolens*, *Bactris* sp., *Basiloxylon* sp., *Bixa orellana*, *Bowdichia virgilioides*, *Bravaisia integerrima*, *Brosimum* sp., *Brownea* sp., *Bursera simaruba*, *Byrsonima* sp., *Calophyllum brasiliense*, *Carapa guianensis*, *Cassia spectabilis*, *Castilla elastica*, *Catostemma commune*, *Cecropia* sp., *Cedrela fissilis*, *Ceiba pentandra*, *Chlorophora tinctoria*, *Cochlospermum* sp., *Cordia alliodora*, *Coumarouna punctata*, *Couratari* sp., *Couroupita guianensis*, *Crescentia cujete*, *Croton* sp., *Didymopanax morotoni*, *Elizabetha princeps*, *Erythrina* sp., *Eschweilera* sp., *Ficus* sp., *Geonoma* sp., *Grislea secunda*, *Guarea trichiloides*, *Guateria* sp., *Guazuma ulmifolia*, *Heliconia* sp., *Hevea* sp., *Hura crepitans*, *Hymenaea courbaril*, *Inga heterophylla*, *I. leiocalycina*, *I. nobilis*, *Iriartea* sp., *Jacaranda* sp., *Jessenia bataua*, *Lantana* sp., *Leopoldinia piassaba*, *Licania* sp., *Luehea candicans*, *L. seemannii*, *Mauritia minor*, *Muntingia calabura*, *Ochroma lagopus*, *Palicourea perquadrangularis*, *Parinarium* (*Parinari*) sp., *Parkia pendula*, *Pentaclethra macroloba*, *Piper* sp., *Protium* sp., *Pterocarpus* sp., *Ricinus* sp., *Sapium* sp., *Scheelea* sp., *Swartzia* sp., *Swietenia macrophylla*, *Tabebuia chrysantha*, *T. pentaphylla*, *Terminalia lucida*, *Trema micrantha*, *Triplaris caracasana*, *Scheelea* sp., *Simaruba amara*, *Socratea* sp., *Sterculia apetala*, *Virola surinamensis*, *Vismia guianensis*, *Vochysia* sp., *Warszewiczia coccinea*, *Xylopia* sp.

9–18. Lower to Upper Montane Broad-Leaved Forest

(Bosque húmedo premontano, bosque muy húmedo premontano, bosque pluvial premontano, bosque seco montano bajo, bosque húmedo montano bajo, bosque muy húmedo montano bajo, bosque pluvial montano bajo, bosque húmedo montano, bosque muy húmedo montano, bosque pluvial montano)

Ferns and allied groups: Cyatheaceae (various tree ferns). Gymnosperms: *Podocarpus macrostachys*, *P. montanus*, *P. oleifolius*, *P. rospigliosii*. Angiosperms: *Acnistus ramiflorus*, *Acrocomia sclerocarpa* (*Cocus aculeatus*), *Aegiphila bogotensis*, *Alchornea grandiflora*, *Alnus jorullensis*, *Anacardium excelsum*, *Annona reticulata*, *Aulomyrcia tomentosa*, *Axinea* sp., *Baccharis nitida*, *B. trinervis*, *Bactris* sp., *Beilschmiedia* sp., *Bejaria aestuans*, *B. glauca*, *Billia columbiana*, *Bocconia frustescens*, *Bonnetia* sp., *Bravaisia integerrima*, *Brunellia integrifolia*, *Buchenavia capitata*, *Bursera tomentosa*, *Byrsonima coriacea*, *Calophyllum brasiliense*, *Cassia jahnii*, *C. spectabilis*, *Cecropia obtusifolia*, *Cedrela mexicana*, *Centropogon alatus*, *Cephalocereus moritzianus*, *Chrysophyllum cainito*, *Chusquea* sp., *Cinchona pubescens*, *Citharexylum* sp., *Clethra bicolor*, *Clusia rosea*, *C. sessilifolia*, *Coccoloba caracasana*, *Comolia* sp., *Cordia alliodora*, *C. caracasana*, *Cornutia microcalycina*, *Croton gossypiifolius*, *Datura* sp., *Dendropanax fendleri*, *Didymopanax morotoni*, *Diplostephium venezuelense*, *Dipterodendron* sp., *Disterigma alaternoides*, *Dodonaea viscosa*, *Drimys granadensis*, *Drosera roraimae*, *Duranta repens*, *Elizabetha macrostachya*, *Erythrina glauca*, *E. poeppigiana*, *Escallonia paniculata*, *E. tortuosa*, *Espeletia neriifolia*, *Euterpe* sp., *Fagara quinduense*, *Faramea killipii*, *Ficus velutina*, *Gaiadendron tagua*, *Gaultheria buxifolia*, *Geissanthus* sp., *Genipa caruto*, *Gliriscidia sepium*, *Grislea secunda*, *Guarea kunthiana*, *Guazuma ulmifolia*, *Guettarda discolor*, *G. gehrigeri*, *G. steyermarkii*, *Gyranthera caribensis*, *Havetia laurifolia*, *Hedyosmum glabratum*, *Heliconia* sp., *Heliocarpus popayanensis*, *Hesperomeles ferruginea*, *Hypericum brathys*, *Ilex* sp., *Inga oerstediana*, *Iriartea* sp., *Jatropha* sp., *Lantana* sp., *Laplacea fruticosa*, *Lecythis* sp., *Lippia hirsuta*, *Lonchocarpus* aff. *margaritensis*, *Luehea candida*, *Mammillaria mamillaria*, *Mauria puberula*, *Melocactus caesius*, *Meriania macrophylla*, *Miconia* sp., *Monnina meridensis*, *Muntingia calabura*, *Myrcia acuminata*, *Myrica pubescens*, *Myriocladus* sp., *Nectandra* sp., *Ochroma lagopus*, *Ocotea* sp., *Opuntia depauperata*, *O. elatior*, *Oreopanax capitatus*, *O. moritzii*, *Ormosia tovarensis*, *Oyedaea verbesinoides*, *Pachira insignis*, *Palicourea crocea*, *P. rigida*, *Pereskia guamacho*, *Piper aduncum*, *P. nobile*, *Pithecellobium saman*, *Poecilochroma lindeniana*, *Polylepis sericea*, *Posoqueria latifolia*, *Protium* sp., *Prunus moritziana*, *P. sphaerocarpa*, *Psidium guianense*, *Pterocarpus podocarpus*, *Rapanea dependens*, *R. ferruginea*, *Rheedia madruno*, *Ricinus communis*, *Rollinia fendleri*, *Roupala complicata*, *R. montana*, *Ryania speciosa*, *Salix humboldtiana*, *Sapindus saponaria*, *Sapium stylare*, *Scheelea* sp., *Schefflera rubiginosa*, *Senecio meridaensis*, *Sipapoa* sp., *Sloanea* sp., *Socratea* sp., *Solanum* sp., *Spondias mombin*, *Symbolanthus tricolor*, *Symplocos* sp., *Tabebuia chrysantha*, *T. pentaphylla*, *Tecoma stans*, *Ternstroemia acrodantha*, *Tibouchina* sp., *Trema micrantha*, *Trichanthera gigantea*, *Triplaris caracasana*, *Turpinia heterophylla*, *Tyleria spectabilis*, *Vaccinium floribundum*, *Vallea stipularis*, *Virola sebifera*, *Vismia ferruginea*, *V. guianensis*, *V. hamanii*, *Vitex compressa*, *Weinmannia jahnii*, *W. microphylla*, *Wigandia caracasana*.

19. Alpine Tundra

(Páramo subalpino, páramo pluvial subalpino, tundra pluvial alpino)

Lichen: *Parmelia mayeri*. Bryophyte (moss): *Leptodontium stellatifolium*. Fern: *Jamesonia* sp. Angiosperms: *Alchemilla* sp., *Alectoridia* sp., *Arenaria* sp., *Calceolaria* sp., *Draba chionophilla*, *Espeletia schultzii*, *Fuchsia* sp., *Gaultheria* sp., *Gentiana nevadensis*, *Halenia* sp., *Hesperomeles* sp., *Hypericum* sp., *Hypochaeris acaulis*, *Lasallia* sp., *Lupinus* sp., *Luzula racemosa*, *Montia meridensis*, *Plantago* sp., *Rhizocephalum* sp., *Senecio* sp., *Vaccinium* sp.

APPENDIX 1.18

Dominant species at Bajo Calima in the Chocó region of western Colombia (based on Faber-Langendoen & Gentry, 1991; see also Forero & Gentry, 1989).

Overstory: *Aspidosperma* sp., *Brosimum utile*, *Calophyllum brasiliense*, *Eschweilera panamensis*, *Goupia glabra*, *Humiriastrum diguense*, *Jessenia bataua*, *Manilkara bidentata*, *Miconia punctata*, *Micropholis crotonoides*, *Otoba lehmannii*, *Pausandra trianae*, *Pouteria buenaventurensis*, *P. eugeniifolia*, *Qualea lineata*, *Socratea exorrhiza*, *Sloanea guianensis*, *Tovomita weddelliana*, *Voychsia* sp., *Welfia georgii*, *Wettinia quinaria*.

Understory: *Faramea* sp., *Mabea occidentalis*, *Macrolobium archeri*, *Miconia centronioides*, *Pausandra trianae*, *Tetrorchidium ochroleucum*.

APPENDIX 1.19

Representative species in the páramo of the Cordillera Oriental of Colombia arranged according to altitudinal-humidity zones (based on Cleef, 1981; van der Hammen & Cleef, 1986; see Fig. 3.134).

Dry Zones

Lower subpáramo (shrub páramo)

Ageratina (*Eupatorium*) *tinifolium*, *Baccharis* sp., *Bejaria* sp., *Brachyotum strigosum*, *Bucquetia glutinosa*, *B. vernicosa*, *Buddleja lindenii*, *Cavendishia* sp., *Coriaria ruscifolia*, *Diplostephium* sp., *Gynoxys* sp., *Hesperomeles* sp., *Macleania rupestris*, *Miconia salicifolia*, *Monnina* sp., *Pentacalia* sp., *Rapanea dependens*, *Sericotheca argentea*, *Solanum bogotense*, *Stevia lucida*.

Upper subpáramo (dwarf shrub páramo)

Altensteinia fimbriata, *A. leucantha*, *Arcytophyllum nitidum*, *Calamagrostis effusa*, *Chaetolepis microphylla*, *Gaylussacia buxifolia*, *Lourteigia microphylla*, *Miconia parvifolia*, *Paepalanthus paramensis*, *Spiranthes vaginata*, *Sporobolus lasiophyllus*, *Verbesina baccharidea*.

Lower páramo (lower bunch grass páramo)

Acaena cylindristachya, *Azorella cuatrecasasii*, *Calamagrostis effusa* (becoming dominant at higher altitudes), *Castratella piloselloides*, *Espeletia* sp., *Espeletiopsis* sp., *Lobelia tenera*, *Luzula racemosa*, *Oreobolus obtusangulus*, *Polylepis incana*, *Rhynchospora paramora*.

Upper páramo (upper bunch grass páramo)

Fern: *Jamesonia bogotensis*. Angiosperms: *Calamagrostis effusa* (closed stands), *C. recta* (mostly higher elevations), *Hypericum selaginella*, *Paepalanthus lodiculoides*.

Lower superpáramo (vegetation becoming sparse)

Lichen: *Cora pavonia*. Musci (mosses): *Bryum capillare*, *Polytrichum juniperinum*, *Zygodon pichinchensis*. Ferns and allied groups: *Jamesonia goudotii*, *Lycopodium crassum*. Angiosperms: *Agrostis boyacensis*, *A. haenkeana*, *Bartsia* sp., *Diplostephium alveolatum*, *D. colombianum*, *D. rhomboidale*, *Draba* sp., *Lachemilla tanacetifolia*, *Loricaria complanata*, *Luzula racemosa*, *Oritrophium cocuyense*, *Pentacalia* (*Senecio*) *andicola*, *P. guicanensis*, *P. vaccinioides*, *Pernettya prostrata*, *Poa* sp.

Upper superpáramo (vegetation sparse)

Musci: *Bryum argenteum*, *Ditrichum gracile*, *Polytrichum juniperellum*, *Racomitrium crispipilum*, *Stereocaulon vesuvianum*. Angiosperms: *Agrostis boyacensis*, *Calamagrostis* sp., *Luzula racemosa*, *Pernettya prostrata*, *Poa* sp., *Senecio* sp.

Humid Slopes

Lower subpáramo

Ageratina (*Eupatorium*) *tinifolium* (abundant), *Aragoa lycopodioides*, *Aulonemia trianae*, *Baccharis* sp., *Centropogon ferrugineus*, *Chusquea scandens*, *Diplostephium* sp., *Escallonia myrtilloides*, *Gaiadendron punctatum*, *Gaultheria ramosissima*, *Hypericum* sp., *Miconia* sp., *Neurolepis aristata*, *Oreopanax* sp., *Purpurella* sp., *Rapanea dependens*, *Symplocos* sp., *Ternstroemia meridionalis*.

Upper subpáramo

Hepaticae (liverworts): *Jamesoniella rubricaulis*, *Lepidozia* sp. Musci: *Campylopus cucullatifolius*, *Rhacocarpus purpurascens*, *Sphagnum magellanicum*, *S. sancto-josephense*. Ferns: *Blechnum* sp., *Lomaria* sp., *Nephopteris maxonii*. Angiosperms: *Ageratina vacciniaefolia*, *Arcytophyllum nitidum*, *Bejaria tachirensis*, *Clethra* sp., *Diplostephium huertasii*, *Disterigma empetrifolium*, *Ilex* sp., *Plutarchia* sp., *Spiranthes coccinea*, *Swallenochloa tessellata*, *Symplocos* sp., *Tofieldia sessiliflora*, *Ugni myricoides*, *Vaccinium floribundum*.

Lower páramo

Lichens: *Cladonia colombiana*, *C. furcata*, *C. polia*. Hepaticae: *Adelanthus lindenbergianus*, *Anastrophyllum* sp., *Cephalozia dussii*, *Herbertus subdentatus*, *Isotachis multiceps*, *Kurzia verrucosa*, *Lepidozia* sp., *Leptoscyphus cleefi*, *Riccardia* sp., *Telaranea nematodes*. Musci: *Breutelia* sp., *Campylopus cavifolius*, *C. cucullatifolius*, *Chorisodontium speciosum*, *Leptodontium wallisii*, *Rhacocarpus purpurascens*, *Sphagnum cuspidatum*, *S. magellanicum*, *S. oxyphyllum*, *S. sancto-josephense*.

Angiosperms: *Arcytophyllum nitidum*, *Calamagrostis effusa*, *Castratella piloselloides*, *C. rosea*, *Lysipomia muscoides*, *Oreobolus obtusangulus*, *Oritrophium peruvianum*, *Paepalanthus pilosus*, *P. lodiculoides*, *Pinguicula elongata*, *Rhynchospora paramora*, *Sisyrinchium pusillum*, *Swallenochloa tessellata* (dominant), *Xyris acutifolia*.

Upper páramo

Fern: *Jamesonia bogotensis* (rare). Angiosperms: *Calamagrostis effusa* (increases), *Cerastium subspicatum*, *Stephaniella* sp., *Swallenochloa tessellata* (decreases).

Lower superpáramo

Lichens: *Cladonia* sp., *Cora pavonia*, *Peltigera* sp., *Siphula* sp., *Sphaerophorus melanocarpus*. Hepaticae: *Anastrophyllum austroamericanum*, *A. nigrescens*, *Cheilolejeunea* sp. Musci: *Bartramia angustifolia*, *Blindia acuta*, *Breutelia integrifolia*, *Campylopus pittieri*, *Distichium capillaceum*, *Erythrophyllopsis andina*, *Gymnomitrion atrofilum*, *Herbertus subdentatus*, *Kingiobryum paramicola*, *Plagiochila dependula*, *Rhacocarpus purpurascens*, *Racomitrium crispulum*, *Zygodon* sp. Ferns: *Hymenophyllum trichophyllum*, *Jamesonia goudotii*. Angiosperms: *Arenaria venezuelana*, *Azorella multifida*, *Cerastium* sp., *Diplostephium rupestre*, *Draba hammenii*, *Erigeron chionophilus*, *E. ecuadoriensis*, *Lachemilla nivalis*, *Lonicera* sp., *Montia meridensis* *Oritrophium peruvianum*, *Ourisia muscosa*, *Senecio niveoaureus*, *Valeriana plantaginea*.

Upper superpáramo

Similar to dry-side superpáramo.

APPENDIX 1.20

Vegetation types of Ecuador according to the classification followed in this text together with the approximately equivalent types used on the vegetation map of Ecuador and in the accompanying text (Sierra, 1999a, b; Sierra et al., 1999). Numbers correspond to those used for vegetation types on the Ecuador map (Fig. 3.138).

Formaciones Naturales de la Costa

Desert

5. Matorral seco—*Achatocarpus pubescens*, *Alternanthera pubiflora*, *Armathocereus* sp., *Bursera graveolens*, *Capparis angulata*, *C. crotonoides*, *C. heterophylla*, *C. mollis*, *Carica parviflora*, *Cochlospermum vitifolium*, *Cordia lutea*, *Croton rivinifolius*, *Erythroxylum glaucum*, *Geoffroea spinosa*, *Heliotropium peruvianum* (*H. arborescens*), *Ipomoea carnea*, *Jacquinia pubescens*, *J. sprucei*, *Loxopterygium huasango*, *Maytenus octogona*, *Monvillea diffusa*, *Muntingia calabura*, *Pisonia aculeata*, *Tillandsia latifolia*, *Vallesia glabra*, *Vriesea barclayana*, *Waltheria ovata*.

Espinar litoral (s.n.; desert vegetation extending onto the coast or on coastal islands)—*Achatocarpus pubescens*, *Arcanthocereus* sp., *Erythroxylum glaucum*, *Hylocereus polyrhizus*, *Malpighia punicifolia*, *Maytenus octogona*, *Monvillea diffusa*, *Pithecellobium excelsum*, *Scutia pauciflora*.

Shrubland/Chaparral–Woodland–Savanna

4. Bosque semideciduo—*Cavanillesia platanifolia*, *Cecropia litoralis*, *Ceiba pentandra*, *C. trichistandra*, *Chrysophyllum argenteum*, *Coccoloba mollis*, *Cochlospermum vitifolium*, *Cynometra bauhinifolia*, *Eriotheca ruizii*, *Eugenia* sp., *Gallesia integrifolia*, *Heliconia latispatha*, *Malmea lucida*, *Philodendron purpureoviride*, *Piper amalago*, *Pithecellobium excelsum*, *Pradosia montana*, *Prosopis juliflora*, *Pseudobombax millei*, *Pseudolmedia rigida*, *Tabebuia billbergii*, *T. chrysantha*, *Trema micrantha*, *Triplaris cumingiana*.

11. Sabana—*Aristida adscensionis*, *Ceiba pentandra*, *C. trichistandra*, *Chloris radiata*, *C. virgata*, *Cochlospermum vitifolium*, *Cyperus iria*, *C. odoratus*, *Echinochloa colonum*, *Eriotheca ruizii*, *Paspalum virgatum*, *Pennisetum occidentale*, *P. purpureum*, *Pseudobombax millei*, *Tragus berteronianus*; in inundated areas *Neptunia oleracea*, *N. plena*; and several trees/shrubs from the bosque semideciduo (*Cavanillesia*, *Pseudobombax*) and the bosque deciduo (*Acacia*, *Mimosa*, *Prosopis*).

Bosque deciduo—Gymnosperm: *Ephedra americana*. Angiosperms: *Acacia* sp., *Albizia multiflora*, *Anthurium barclayanum*, *Armathocereus* sp., *Bombax ruizii*, *Cavanillesia platanifolia*, *Ceiba trichistandra*, *Cochlospermum vitifolium*, *Eriotheca ruizii*, *Gliricidia brenningii*, *Guazuma ulmifolia*, *Hylocereus polyrhizus*, *Machaerium millei*, *Mimosa albida*, *M. pigra*, *Muntingia calabura*, *Prosopis juliflora*, *Pseudobombax millei*, *Simira ecuadorensis*, *Tabebuia billbergii*, *T. chrysantha*, *Tecoma castanifolia*, *Trichilia hirta*; disturbed areas: *Acnistus arborescens*, *Celtis iguanaea*.

Mangrove

1. Manglar—Fern: *Polypodium bombycinum*. Angiosperms: *Aechmea pyramidalis*, *Avicennia germinans*, *Conocarpus erectus*, *Guzmania monostachya*, *Laguncularia racemosa*, *Lockhartia serra*, *Pelliceria rhizophorae*, *Rhizophora harrisonii*, *R. mangle*, *Tillandsia usneoides*.

Beach/Strand/Dune

Matorral seco litoral (s.n.)—*Batis maritima*, *Canavalia maritima*, *Cryptocarpus pyriformis*, *Hippomane mancinella*, *Ipomoea pes-caprae*, *Lycium minimum*, *Maytenus octogona*, *Scaevola plumieri*, *Sesuvium portulacastrum*, *Vallesia glabra*.

Freshwater Herbaceous Bog/Marsh/Swamp

5. Herbazal—*Bolbitis pandurifolia*, *Canna paniculata*, *Ceratophyllum demersum*, *Corchorus orinocensis*, *Cyperus odoratus*, *Echinodorus bracteatus*, *Eichornia crassipes*, *Hydrocleys nymphoides*, *Fimbristylis dichotoma*, *Hydrocotyle ranunculoides*, *Hydrolea spinosa*, *Lemna minima*, *Limnobium laevigatum*, *Limnocharis flava*, *Ludwigia octovalis*, *Mariscus ligularis*, *Neptunia prostrata*, *Nymphaea blanda*, *Paspalum conjugatum*, *Pistia stratiotes*, *Rhynchospora scutellata*, *Thalia geniculata*,

Typha dominguensis, *Xanthosoma sagittifolium*; bordering trees include *Cariodaphnopsis theobromifolia* and *Euterpe chaunostachys*.

Aquatic (included under herbazal)—Fern: *Ceratopteris pteridoides*. Angiosperms: *Ceratophyllum demersum*, *Eichornia crassipes*, *Hydrocleys nymphoides*, *Lemna minima*, *Limnobium laevigatum*, *Nymphaea blanda*, *Pistia stratiotes*.

Lowland Neotropical Rain Forest

2. Bosque siempreverde inundable—*Amanoa anomala*, *Carapa guianensis*, *Entada gigas*, *Euterpe chaunostachys*, *Genipa americana*, *Inga punctata*, *Mora megistosperma*, *Otoba gordoniifolia*, *Pterocarpus officinalis*, *Symphonia globulifera*.

3. Bosque siempreverde—Gymnosperm: *Zamia lindenii*. Angiosperms: *Astrocaryum standleyanum*, *Brosimum utile*, *Brownea multijuga*, *Calathea lutea*, *Carapa guianensis*, *Caryodaphnopsis theobromifolia*, *Castilla elastica*, *Ceiba pentandra*, *Clarisia racemosa*, *Conostegia cuatrecasii*, *Coussapoa villosa*, *Cybianthus kayapii*, *Ficus obtusifolia*, *Guarea polymera*, *Humiriastrum procerum*, *Inga silanchensis*, *Iriartea deltoidea*, *Lecythis ampla*, *Nectandra guadaripo*, *Otoba gordoniifolia*, *Perebea xanthochyma*, *Phytelephas aequatorialis*, *Poulsenia armata*, *Rhodospatha densinervia*, *Swartzia haughtii*, *Tectaria incisa*, *Tetrathylacium macrophyllum*, *Theobroma gileri*, *Tillandsia narthecioides*, *Virola sebifera*, *Wettinia quinaria*, *Xanthosoma daguense*.

Lower to Upper Montane Broad-Leaved Forest

7, 8. Bosque siempreverde piemontano—Fern (disturbed areas): *Lophosoria quadripinnata*. Angiosperms: *Bactris setulosa*, *Brownea coccinea*, *Carapa guianensis*, *C. megistocarpa*, *Carludovica palmata*, *Caryodaphnopsis theobromifolia*, *Castilla elastica*, *Chamaedorea pinnatifrons*, *C. poeppigiana*, *Clarisia racemosa*, *Coussapoa villosa*, *Erythrina edulis*, *Erythrochiton carinatus*, *E. giganteus*, *Eschweilera rimbachii*, *Faramea occidentalis*, *Ficus obtusifolia*, *Geonoma macrostachys*, *Guadua angustifolia*, *Guarea cartaguenya*, *Heisteria acuminata*, *Hirtella mutisii*, *Iriartea deltoidea*, *Mabea occidentalis*, *Matisia soegengii*, *Ocotea sodiroana*, *Otoba gordoniifolia*, *Perebea xanthochyma*, *Pholidostachys dactyloides*, *Phytelephas aequatorialis*, *Pourouma bicolor*, *Protium occidentalis*, *Pseudolmedia rigida*, *Quararibea asterolepis*, *Sorocea sarcocarpa*, *Swartzia haughtii*, *Wettinia equalis*, *W. quinaria*, *Virola dixoni*, *V. elongata*, *V. sebifera*, *Vitex gigantea*. Subcanopy: *Anthurium pallidiflorum*, *Heliconia stricta*, *Heteropsis ecuadorensis*, *Ossaea micrantha*, *Palicourea demissa*, *Philodendron purpureoviride*, *Trichilia surinamensis*, *Xanthosoma daguense*. Herbs: *Costus laevis*, *Irlbachia alata*.

10. Bosque semideciduo piemontano—*Anthurium barclayanum*, *Capparis* sp., *Cecropia litoralis*, *Cedrela odorata*, *Chrysophyllum argenteum*, *Coccoloba mollis*, *Cochlospermum vitifolium*, *Cynometra bauhinifolia*, *Eugenia* sp., *Gallesia integrifolia*, *Malmea lucida*, *Plumbago scandens*, *Pradosia montana*, *Pseudolmedia rigida*, *Sorocea sprucei*, *Trema micrantha*, *Triplaris cumingiana*. Disturbed areas: *Acnistus arborescens*.

13. Bosque de neblina montano bajo—Ferns: *Alsophila cuspidata*, *Cyathea bipinnatifida*. Angiosperms: *Alchornea iricurana*, *Asplundia peruviana*, *Beilschmiedia alloiophylla*, *Brunellia acostae*, *Columnea densibracteata*, *C. minor*, *Conostegia cuatrecasii*, *C. montana*, *Guzmania angustifolia*, *Hedyosmum sprucei*, *Hieronyma duquei*, *Metteniusa nucifera*, *Myrsine pellucida*, *Phytolacca dioica*, *Symplocos ecuadorensis*.

Formaciones Naturales de la Sierra

Shrubland/Chaparral–Woodland–Savanna

17, 32. Matorral seco montano—*Acacia macracantha*, *Caesalpinia spinosa*, *Croton elegans*, *C. wagneri*, *Dodonaea viscosa*, *Mimosa quitensis*, *Opuntia pubescens*, *O. soederstromiana*, *O. tunicata*, *Talinum paniculatum*, *Tecoma stans*; in more humid sites: *Salix humboldtiana*, *Schinus molle*, *Tillandsia recurvata*, *T. secunda*; espinar seco montano—*Acacia macracantha*, *Capparis flexuosa*, *Chorisia* sp., *Cleistocactus icosagonus*, *C. leonensis*, *C. sepium*, *Eriotheca ruizii*, *Opuntia pubescens*, *O. soederstromiana*, *O. tunicata*.

Freshwater Herbaceous Bog/Marsh/Swamp

22. Herbazal lacustre montano—Ferns and allied groups: *Isoetes* aff. *lechleri*. Angiosperms: *Crassula venezuelensis*, *Elatine ecuadoriensis*, *Isolepis inundata*, *Juncus arcticus*, *J. stipulatus*, *Scirpus californicus*.

Aquatic (included under herbazal)—*Callitriche deflexa*, *Myriophyllum quitense*, *Potamogeton filiformis*, *P. striatus*.

30. Herbazal lacustre montano alto—*Crassula venezuelensis*, *Elatine ecuadoriensis*, *Isolepis inundata*, *Juncus arcticus*, *J. stipulatus*, *Scirpus californicus*.

Lower to Upper Montane Broad-Leaved Forest

16. Matorral seco montano bajo (driest; transition to shrubland/chaparral–woodland–savanna)—*Acacia macracantha*, *Capparis flexuosa*, *C. millei*, *Ceiba* sp., *Chorisia* sp., *Croton wagneri*, *Dodonaea viscosa*, *Eriotheca ruizii*, *Mimosa quitensis*, *Opuntia* sp., *Salix humboldtiana*, *Schinus molle*, *Tabebuia chrysantha*.

18. Bosque siempreverde montano bajo—Fern: *Cyathea* sp. Angiosperms: *Anthurium ovatifolium*, *Buddleja americana*, *Carapa guianensis*, *Casearia* sp., *Cecropia andina*, *C. bullata*, *C. hachensis*, *C. monostachya*, *Cedrela odorata*, *Ceroxylon alpinum*, *C. echinulatum*, *Chusquea* sp., *Dictyocaryum lamarckianum*, *Elaeagia* sp., *Ficus* sp., *Fuchsia macrostigma*, *Geonoma weberbaueri*, *Guarea kunthiana*, *Hedyosmum* sp., *Heliconia* sp., *Miconia porphyrotricha*, *Morus insignis*, *Nectandra membranacea*, *Ocotea* sp., *Piper* sp., *Sapium utile*, *Siparuna eggersii*, *S. guajalitensis*, *S. laurifolia*, *Socratea exorrhiza*.

19. Bosque de neblina montano—Ferns: *Blechnum monomorphum*, *Cyathea caracasana*, *Dennstaedtia kalbreyeri*, *D. paucirrhiza*, *D. producta*, *D. tryoniana*. Angiosperms: *Aegiphila* sp., *Alnus acuminata*, *Anthurium gualeanum*, *A. microspadix*, *A. mindense*, *A. nanegalense*, *A. penningtonii*, *Barnadesia parviflora*, *Begonia* sp., *Bocconia integrifolia*, *Bomarea* sp., *Brachyotum ledifolium*, *Brunellia tomentosa*, *Cecropia maxima*, *Cedrela montana*, *Ceroxylon ventricosum*, *Chusquea scandens*, *Elaeagia utilis*, *Erythrina edulis*, *Escallonia paniculata*, *Freziera verrucosa*, *Fuchsia pilaloensis*, *F. scabriuscula*, *Geonoma weberbaueri*, *Gunnera brephogea*, *G. colombiana*, *Hieronyma macrocarpa*, *Juglans neotropica*, *Miconia corazonica*, *M. crocea*, *M. theizans*, *Myrcianthes hallii*, *Nectandra* sp., *Palicourea* sp., *Passiflora*

alnifolia, *P. coactilis*, *P. mixta*, *Peperomia* sp., *Piper carpunya*, *P. sodiroi*, *Prestoea acuminata*, *Siparuna guajalitensis*, *S. piloso-lepidota*, *Weinmannia pinnata*.

20. Bosque siempreverde montano alto—*Axinaea quitensis*, *Berberis conferta*, *Brachyotum gracilescens*, *B. ledifolium*, *Buddleja incana*, *B. multiceps*, *B. pichinchensis*, *Cervantesia tomentosa*, *Freziera canescens*, *F. verrucosa*, *Gunnera pilosa*, *Gynoxys buxifolia*, *G. chingualensis*, *G. fuliginosa*, *Hedyosmum luteynii*, *Hesperomeles lanuginosa*, *Hypericum laricifolium*, *Lupinus* sp., *Miconia barclayana*, *Myrcianthes rhopaloides*, *Oreopanax* sp., *Piper* sp., *Polylepis* sp., *Siparuna echinata*, *Siphocampylus giganteus*, *Tournefortia fuliginosa*, *T. scabrida*, *Vallea stipularis*.

26. Bosque siempreverde montano bajo—Fern: *Cyathea* sp. Gymnosperm: *Podocarpus sprucei*. Angiosperms: *Ageratum iltisii*, *Anthurium grex-avium*, *Axinaea pauciflora*, *Bejaria zamorae*, *Cecropia montana*, *Centropogon quebradanus*, *Columnea flexiflora*, *Epidendrum neolehmannia*, *Ficus* sp., *Fuchsia* sp., *Heliconia* sp., *Hieronyma macrocarpa*, *Lepanthes auriculata*, *Miconia cosangensis*, *Piper* sp., *Siparuna cascada*.

27. Bosque de neblina montano—Ferns and allied groups: *Cyathea* sp., *Dennstaedtia macrosora*, *Dicksonia stuebelli*, *Huperzia austroecuadorica*, *H. campiana*, *H. kuesteri*, *H. loxensis*. Gymnosperm: *Podocarpus oleifolius*. Angiosperms: *Ageratina dendroides*, *Aiouea dubia*, *Alnus acuminata*, *Anthurium corrugatum*, *A. lennartii*, *A. marginatum*, *Aphelandra acanthifolia*, *A. chrysantha*, *Axinaea sclerophylla*, *Begonia* sp., *Bejaria resinosa*, *Berberis* sp., *Bomarea comata*, *B. setacea*, *Brachionidium loxense*, *Brachyotum* sp., *Brunellia zamorensis*, *Cecropia angelica*, *C. villosa*, *Centropogon comosus*, *C. heteropilis*, *Ceratostema alatum*, *Ceroxylon parvifrons*, *C. vogelianum*, *Chusquea falcata*, *Cinchona lucumifolia*, *C. mutisii*, *C. rugosa*, *Columnea eubracteata*, *Drimys granadensis*, *Elaeagia ecuadorensis*, *Epidendrum* sp., *Escallonia paniculata*, *Fuchsia* sp., *Geonoma lindeniana*, *Gunnera* sp., *Hedyosmum translucidum*, *Lepanthes grossiradix*, *Lupinus* sp., *Mauria simplicifolia*, *Miconia caesearita*, *M. capitellata*, *M. dodsonii*, *M. rivetii*, *M. zamorensis*, *Ocotea arnottiana*, *O. benthamiana*, *O. smithiana*, *Oreocallis grandiflora*, *Oreopanax andreanus*, *O. eriocephalus*, *O. sessiliflorus*, *Passiflora sprucei*, *Peperomia* sp., *Persea subcordata*, *Piper* sp., *Pleurothallis obovata*, *P. tritis*, *Ruagea microphylla*, *Rubus adenothallus*, *Saurauia lehmannii*, *Schefflera* sp., *Serjania paniculata*, *Sticherus penniger*, *Tibouchina oroensis*. At the lower altitudinal limits: *Aiphanes grandis*, *Begonia tropaeolifolia*, *Brunellia ovalifolia*, *Carica omnilingua*, *Centropogon* sp., *Ceroxylon alpinum*, *Gynoxys jaramilloi*, *Psammisia ecuadorensis*, *Siphocampylus humboldtianus*, *Verbesina pentantha*, *Weinmannia* sp. At the upper altitudinal limits: *Brachyotum* sp., *Hypericum laricifolium*, *Miconia* sp.

20. Bosque siempreverde montano alto—Fern: *Dicksonia sellowiana*. Angiosperms: *Ageratina dendroides*, *Aiouea dubia*, *Bejaria resinosa*, *Bomarea brachysepala*, *Brachyotum andreanum*, *Brunellia ovalifolia*, *Cavendishia* sp., *Cinchona officinalis*, *Clethra ovalifolia*, *C. revoluta*, *Freziera microphylla*, *Gynoxys regis*, *Meriana* sp., *Miconia* sp., *Ocotea infrafoveolata*, *Oreopanax impolitus*, *O. obscurus*, *O. sessiliflorus*, *Pentacalia theifolia*, *Persea* sp., *Psychotria* sp., *Ruagea hirsuta*, *Siparuna petiolaris*, *Symplocos clethrifolia*, *S. fuscata*, *Ternstroemia macrocarpa*, *Weinmannia elliptica*, *Zinowiewia madsenii*. Transition to páramo (ceja): *Hypericum laricifolium*, *Lupinus* sp.

31. Matorral húmedo montano—Ferns: *Elaphoglossum* sp., *Polypodium* sp. Angiosperms: *Alnus acuminata*, *Baccharis alaternoides*, *B. buxifolia*, *B. oblongifolia*, *B. prunifolia*, *Blakea oldemanii*, *Brachyotum confertum*, *Brugmansia arborea*, *Calceolaria adenanthera*, *C. crenata*, *Cedrela lilloi*, *Cestrum peruvianum*, *C. quitense*, *C. tomentosum*, *Cleome longifolia*, *Cordia rusbyi*, *Coriaria ruscifolia*, *Croton wagneri*, *Erythrina edulis*, *Ilex lechleri*, *I. rupicola*, *Juglans neotropica*, *Lantana rugulosa*, *Miconia crocea*, *Ocotea rotundata*, *Odontoglossum gracile*, *Oreocallis grandiflora*, *O. mucronata*, *Oreopanax avicenniifolius*, *O. confusus*, *O. corazonensis*, *Panopsis ferruginea*, *Paspalum humboldtianum*, *Persea ferruginea*, *Solanum crinitipes*, *Symplocos* sp., *Tibouchina laxa*.

32. Matorral húmedo montano bajo—*Anthurium cutucuense*, *A. santiagoense*, *Baccharis jelskii*, *Bonnetia paniculata*, *Calathea plurispicata*, *Cecropia pastasana*, *Codonanthe erubescens*, *Costus zamoranus*, *Daphnopsis zamorensis*, *Guzmania asplundii*, *Lepanthes narcissus*, *Meriania cuneifolia*, *Miconia imitans*, *Myrcia* sp., *Myrcianthes* sp., *Ocotea* sp., *Oreopanax microflorous*, *Passiflora telesiphe*, *Persea* sp., *Pitcairnia andreetae*, *Pleurothallis* sp., *Saurauia crassisepala*, *Ternstroemia* sp., *Thibaudia harlingii*, *Weinmannia* sp. In the underbrush: *Asplundia helicotricha*, *A. schizotepala*.

33. Bosque semideciduo montano bajo—*Aiphanes grandis*, *Anthurium angustilaminatum*, *A. ovatifolium*, *Bocconia* aff. *integrifolia*, *Brugmansia versicolor*, *Carapa megistocarpa*, *Cecropia litoralis*, *Ficus* sp., *Fuchsia* sp., *Heliconia* sp., *Miconia denticulata*, *Piper* sp., *Pleurothyrium obovatum*, *Sapium* sp., *Saurauia tambensis*, *Siparuna croati*, *S. eggersii*, *Sobralia oroana*, *Tabebuia chrysantha*.

Páramo

21. Páramo herbáceo—Ferns and allied groups: *Cyathea* sp., *Huperzia hypogaea*, *H. talpiphila*, *Lycopodium* sp. Angiosperms: *Agrostis breviculmis*, *Azorella* sp., *Baccharis caespitosa*, *Befaria resinosa*, *Calamagrostis effusa*, *C. macrophylla*, *Castilleja* sp., *Chuquiraga insignis*, *C. jussieui*, *Festuca* sp., *Gentiana sedifolia*, *Gentianella cerastioides*, *G. selaginifolia*, *Geranium ecuadoriense*, *G. sericeum*, *Halenia* sp., *Hypochaeris* sp., *Lachemilla orbiculata*, *Lupinus smithianus*, *Neurolepis laegaardii*, *N. nana*, *Oritrophium peruvianum*, *Polylepis* sp., *Ranunculus guzmannii*, *R. praemorsus*, *Stipa rosea*, *Valeriana aretioides*, *V. bracteata*, *V. convallarioides*, *V. imbricata*, *V. microphylla*, *V. rigida*, *Werneria nubigena*.

22. Páramo de frailejones (*Espeletia*)—*Agrostis tolucensis*, *Azorella* sp., *Baccharis teindalensis*, *Calamagrostis intermedia*, *Diplostephium floribundum*, *Eriocaulon microcephalum*, *Espeletia pycnophylla*, *Festuca* sp., *Oreopanax sodiroi*, *Pentacalia andicola*, *Polylepis incana*, *P. pauta*, *Stipa ichu*, *Werneria crassa*, *W. pumila*.

23. Páramo seco—Gymnosperm: *Ephedra americana*. Angiosperms: *Astragalus geminiflorus*, *Azorella pedunculata*, *Calandrinia acaulis*, *Calceolaria ericoides*, *Chuquiraga jussieui*, *Culcitium nivale*, *Hypochaeris sonchoides*, *Lupinus microphyllus*, *Nototriche pichinchensis*, *Poa cucullata*, *Polylepis microphylla*, *Senecio comosus*, *S. microdon*, *Stipa hans-meyeri*, *S. ichu*. In the driest parts: *Astragalus* sp., *Loricaria ilinissae*.

24. Gelidafria (coldest páramo)—Lichens: *Gyrophora* sp., *Lecanora* sp. Musci: *Grimmia* sp. Angiosperms: *Aciachne flagellifera*, *Calamagrostis ecuadoriensis*, *C. guamanensis*, *Draba aretioides*, *Loricaria ferruginea*, *Valeriana pilosa*.

29. Páramo de almohadillas (cushion plants)—Gymnosperm: *Ephedra rupestris*. Angiosperms: *Azorella aretioides*, *A. corymbosa*, *A. pedunculata*; associated non-cushion plants. Musci: *Sphagnum*. Ferns and related groups: *Huperzia hypogaea*, *H. llanganatensis*, *Isoetes* sp., *Jamesonia* sp., *Lycopodium* sp. Angiosperms: *Baccharis* sp., *Chuquiraga jussieui*, *Culcitium* sp., *Diplostephium rupestre*, *Distichia acicularis*, *Draba aretioides*, *Gentiana* sp., *Halenia* sp., *Hesperomeles obtusifolia*, *Lachemilla orbiculata*, *Loricaria* sp., *Oritrophium* sp., *Plantago rigida*, *Senecio* sp., *Valeriana* sp., *Viola* sp., *Werneria humilis*, *W. nubigena*.

35. Páramo arbustivo (shrubby páramo)—Musci: *Sphagnum* sp. Ferns and allied groups: *Isoetes* sp., *Jamesonia* sp., *Lycopodium* sp. Angiosperms: *Azorella aretioides*, *A. corymbosa*, *A. pedunculata*, *Baccharis* sp., *Chuquiraga jussieui*, *Culcitium* sp., *Diplostephium rupestre*, *Distichia tolimensis*, *Draba aretioides*, *Gentiana* sp., *Halenia* sp., *Lachemilla orbiculata*, *Loricaria* sp., *Lupinus* sp., *Plantago rigida*, *Senecio* sp., *Siphocampylus asplundii*, *Valeriana* sp., *Viola* sp., *Werneria humilis*, *W. nubigena*.

Formaciones Naturales de la Amazonia

Freshwater Herbaceous Bog/Marsh/Swamp

39. Herbazal—*Cyperus odoratus*, *Ludwigia octovalvis*, *Montrichardia linifera*, *Pontederia rotundifolia*, *Sagittaria* sp.

Lowland Neotropical Rain Forest

36. Bosque siempreverde; 37. Bosque siempreverde de palmas inundable; 38. Bosque siempreverde inundable—*Acacia glomerosa* (higher, drier sites), *Astrocaryum jauari*, *Bactris riparia*, *Buchenavia* sp., *Calathea* sp., *Calliandra angustifolia*, *Calycophyllum spruceanum*, *Caryodendron orinocense*, *Cecropia* sp., *Cedrelinga cateniformis*, *Ceiba pentandra*, *Chorisia insignis*, *Clidemia* sp., *Croton cuneatus*, *C. tessmannii*, *Dictyoloma peruvianum*, *Dieffenbachia* sp., *Eschweilera coriacea*, *Ficus insipida*, *Genipa spruceana*, *Grias peruviana*, *Guarea guidonia*, *G. kunthiana*, *G. macrophylla*, *Gynerium sagittatum*, *Hasseltia floribunda*, *Iriartea deltoidea*, *Macrolobium acaciifolium*, *Matisia obliquifolia*, *Mauritia flexuosa*, *Mauritiella aculeata*, *Myrciaria dubia*, *Neosprucea grandiflora*, *Oenocarpus bataua*, *Otoba glycycarpa*, *O. parvifolia*, *Parkia multijuga*, *Philodendron* sp., *Pourouma bicolor*, *P. minor*, *Protium fimbriatum*, *Pseudolmedia macrophylla*, *Pterocarpus amazonicus*, *Sapium* sp., *Scheelea brachyclada*, *Senefeldera inclinata*, *Senna spinescens*, *Simira cordifolia*, *Sterculia apetala*, *Terminalia amazonia*, *T. oblonga*, *Tessaria integrifolia*, *Tetrathylacium macrophyllum*, *Tovomitopsis membranacea*, *Trichilia laxipaniculata*, *Virola calophylla*, *V. duckei*, *V. surinamensis*, *Warszewiczia coccinea*.

Lower to Upper Broad-Leaved Montane Forest

40. Bosque siempreverde piemontano—Gymnosperm: *Podocarpus* sp. Angiosperms: *Bambusa* sp., *Brunellia* sp., *Caryodendron orinocense*, *Catoblastus praemorsus*, *Ceiba pentandra*, *Ceroxylon* sp., *Clarisia racemosa*, *Dacryodes cupularis*, *Erisma uncinatum*, *Guarea persistens*, *Gyranthera* sp., *Hedyosmum* sp., *Heisteria acuminata*, *Iriartea deltoidea*, *Leonia glycycarpa*, *Ocotea javitensis*, *Oenocarpus bataua*, *Otoba glycycarpa*, *Pourouma guianensis*, *Remijia* sp., *Ruagea glabra*, *Saurauia* sp., *Vochysia ferruginea*, *Weinmannia* sp., *Wettinia maynensis*.

41. Bosque siempreverde montano bajo—*Alchornea leptogyna*, *Billia columbiana*, *Cedrela odorata*, *Dacryodes* sp., *Dictyocaryum lamarckianum*, *Guarea kunthiana*, *Meriania hexamera*, *Ocotea javitensis*, *Otoba glycycarpa*.

42. Matorral húmedo montano—*Alchornea* sp., *Blakea* sp., *Ilex* sp., *Miconia* sp., *Weinmannia* sp.

43. Matorral húmedo montano alto—*Blakea* sp., *Bonnetia paniculata*, *Dacryodes* sp., *Elaeagia mariae*, *E. pastoense*, *Mollinedia* sp., *Persea* sp., *Ternstroemia* sp.

APPENDIX 1.21

Vegetation types of Bolivia arranged according to the classification followed in this text together with the approximately equivalent types and representative species in Killeen et al. (1993).

Shrubland/Chaparral–Woodland–Savanna

Valles secos interandinos (elevation 500–3300 m, MAP 500–600 mm, annual temperatures 2°–[12°–16°]–28° C)—*Acacia macracantha*, *Aspidosperma quebracho-blanco*, *Astronium urundeuva*, *Athyana weinmanniifolia*, *Baccharis dracunculifolia*, *Cardenasiodendron brachypterum*, *Carica quercifolia*, *Ceiba tunariense*, *Cereus comarapanus*, *Dodonaea viscosa*, *Erythrina falcata*, *Eupatorium buniifolium*, *Jacaranda mimosifolia*, *Kageneckia lanceolata*, *Kentrothamnus weddellianus*, *Loxopterygium grisebachii*, *Neoraimondia herzogiana*, *Opuntia* sp., *Parajubaea torallyi*, *Prosopis kuntzei*, *Pseudobombax andicola*, *Samaipaticereus corroanus*, *Schinopsis haenkeana*, *Schinus molle*, *Tipuana tipu*.

Sabanas húmedas (130–250 m, MAP 1000–2000 mm, MAT 26° C)—*Acacia* sp., *Acrocomia aculeata*, *Apeiba tibourbou*, *Bunchosia* sp., *Calophyllum brasiliense*, *Copaifera reticulata*, *Copernicia alba*, *Cupania cinerea*, *Curatella americana*, *Ficus* sp., *Genipa americana*, Gramineae (*Andropogon*, *Coelorachis*, *Eriochrysis*, *Imperata*, *Leersia*, *Paspalum*), *Guarea macrophylla*, *Guazuma ulmifolia*, *Hymenea courbaril*, *Inga* sp., *Leuhea paniculata*, *Licania octandra*, *Machaerium hirtum*, *Mauritiella aculeata*, *Peschiera arcuata*, *Pseudobombax marginatum*, *Rheehia achachairu*, *Scheelea princeps*, *Sorocea sprucei*, *Spondias lutea*, *Sterculia stricta*, *Swartzia jorori*, *Tabebuia aurea*, *T. heptaphylla*, *T. insignis*, *T. impetiginosa*, *Triplaris americana*, *Virola sebifera*, *Xylosma benthamii*.

Bosque seco chaqueño y bosque serrano chaqueño (Bolivian

part of the Grand Chaco; 300–600 m, MAP 500–1000 mm, MAT 22°–26° C, range 48°–1° C)—Angiosperms: *Acacia* sp., *Aspidosperma quebracho-blanco*, *Astronium urundeuva*, *Bougainvillea infesta*, *B. praecox*, *Caesalpinia paraguariensis*, *Calycophyllum multiflorum*, *Capparis* sp., *Celtis spinosa*, *Cereus dayamii*, *Chorisia insignis*, *Cochlospermum tetraporum*, *Geoffroea decorticans*, *Gleditsia amorphoides*, *Jodina rhombifolia*, *Lithraea ternifolia*, *Pereskia sacharosa*, *Prosopis alba*, *P. nigra*, *Ruprechtia triflora*, *Sambucus australis*, *Schinopsis cornuta*, *S. haenkeana*, *S. quebracho-colorado*, *Stetsonia coryne*, *Trithrinax schizophylla*, *Vallesia glabra*, *Zanthoxylum coco*, *Ziziphus mistol*.

Campos Amazónicos (Lowland Grasslands)

Campos cerrados (MAP 1000 mm, MAT 22° C)—*Aspidosperma nobile*, *Byrsonima chrysophylla*, *Callisthene fasciculata*, *Caryocar brasiliense*, *Didymopanax* sp., *Dimorphandra gardneriana*, *Dipteryx alata*, *Eriotheca gracilipes*, Gramineae (*Andropogon*, *Axonopus*, *Elionurus*, *Paspalum*, *Schizachyrium*), *Lafoensia pacari*, *Qualea multiflora*.

Freshwater herbaceous bog/marsh/swamp (included under sabanas húmedas; see also Ritter, 2004, ref. Chapter 3)—*Cyperus giganteus*, *Thalia geniculata*.

Lowland Neotropical Rain Forest

Bosque amazónico (elevation 100–250 m, MAP 1800–2200 mm, MAT 25°–27° C)—*Apuleia leiocarpa*, *Astrocaryum chonta*, *A. macrocalyx*, *Bertholletia excelsa*, *Calophyllum brasiliense*, *Castilla ulei*, *Ceiba pentandra*, *Chelyocarpus chuco*, *Couratari guianensis*, *Dialium guianense*, *Dipteryx micrantha*, *Enterolobium contortisiliquum*, *Ficus* sp., *Guadua* sp., *Hevea brasiliensis*, *Iriartea deltoidea*, *Manilkara bidentata*, *Mauritia flexuosa*, *Mezilaurus itauba*, *Oenocarpus mapora*, *Phenakospermum guianensis*, *Phytelephas macrocarpa*, *Tachigali* sp., *Theobroma speciosum*.

Lower to Upper Montane Broad-Leaved Forest

Bosque montano húmedo y ceja de monte yungueña (yungas, transition to shrub tundra; 400–2800 m [ceja 2700–3200 m], MAP 2000–5000 mm [ceja 2500–3500 mm], MAT 17°–24° C [ceja 10°–14° C])—Fern: *Cyathea caracasana*. Gymnosperm: *Podocarpus* (*Prumnopitys*) *ingensis*. Angiosperms: *Astrocaryum macrocalyx*, *Ceroxylon* sp., *Cinchona calisaya*, *C. officinalis*, *Clarisia racemosa*, *Clethra scabra*, *Dendropanax* sp., *Dictyocaryum lamarckianum*, *Inga* sp., *Iriartea deltoidea*, *Miconia* sp., *Myrsine coriacea*, *Oreopanax membranaceus*, *Poulsenia armata*, *Protium* sp., *Tetragastris altissima*, *Weinmannia crassifolia*. Ceja—Musci: *Sphagnum*. Fern: *Gleichenia*. Angiosperms: *Chusquea* (bamboo), *Escallonia* sp., *Freziera* sp., *Gaiadendron punctatum*, *Gynoxys* sp., *Morella pubescens*, *Oreopanax pentlandianus*, *Persea ruizii*, *Polylepis pepei*, *Prunus brittoniana*, *Saracha punctata*, *Thibaudia crenulata*, *Weinmannia bangii*, *W. sorbifolia*.

Bosque Tucumano–Boliviano (800–3000 m, MAP 1000–1700 mm, MAT 13° [uplands]–23° C [lowlands])—Gymnosperm: *Podocarpus parlatorei*. Angiosperms: *Alnus acuminata*, *Blepharocalyx salicifolius*, *Cedrela lilloi*, *Cinnamomum porphyrium*, *Escallonia hypoglauca*, *Juglans australis*, *Morella pubescens*, *Myrcianthes pseudomato*, *Myrsine coriacea*, *Polylepis besseri*, *Prunus tucumanensis*, *Sambucus australis*, *Zanthoxylum coco*.

Bosque semideciduo chiquitano (transition between the lowland rain forest and the drier Grand Chaco; 300–1200 m, MAP 1000–1500 mm, MAT 23° C)—*Anadenanthera colubrina*, *Aspidosperma cylindrocarpon*, *Astronium fraxinifolium*, *A. urundeuva*, *Bougainvillea modesta*, *Cereus* sp., *Chorisia speciosa*, *Chrysophyllum gonocarpum*, *Cordia alliodora*, *Gallesia integrifolia*, *Guadua paniculata*, *Machaerium scleroxylon*, *Orbignya phalerata*, *Phyllostylon rhamnoides*, *Schinopsis brasiliensis*, *Tabebuia chrysantha*, *T. impetiginosa*, *Terminalia argentea*.

Bosque húmedo del escudo precámbrico (to 1000 m)—*Ampelocera ruizii*, *Bertholletia excelsa*, *Calycophyllum spruceanum*, *Euterpe precatoria*, *Gallesia integrifolia*, *Hura crepitans*, *Jacaratia spinosa*, *Ocotea guianensis*, *Schizolobium amazonicum*, *Swietenia macrophylla*, *Syagrus sancona*, *Terminalia oblonga*.

Bosque húmedo de llanura (150–250 m, MAP 1200–1800 mm, MAT 25° C)—*Bactris gasipaes*, *Calycophyllum spruceanum*, *Clarisia racemosa*, *Erythrina fusca*, *Ficus* sp., *Guarea macrophylla*, *Guatteria* sp., *Hura crepitans*, *Iriartea deltoidea*, *Jessenia bataua*, *Pourouma guianensis*, *Protium sagotianum*, *Pseudolmedia laevis*, *Rheedia achachairu*, *Salacia impressifolia*, *Scheelea princeps*, *Sloanea guianensis*, *Socratea exorrhiza*, *Swietenia macrophylla*, *Symphonia globulifera*, *Terminalia oblonga*, *Trichilia pleeana*, *Xylopia ligustrifolia*.

Alpine Tundra (Páramo)

Puna y vegetación altoandina, including bosquecillos de *Polylepis* (the high-altitude secondary vegetation is locally called thola, the common name for *Baccharis*; 2500–4800 m, MAP 500 mm, MAT <10° C)—*Baccharis*, *Berberis*, *Buddleja*, *Citharexylum*, *Colletia*, *Duranta*, *Escallonia*, Gramineae (*Calamagrostis*, *Festuca*, *Stipa*), *Myrcianthes*, *Polylepis*, *Senna*.

APPENDIX 1.22

Plant formations and representative species in the vegetation of Chile (based on Marticorena & Rodríguez, 1995 et seq., and various sources).

Desert (Antafagasto and vicinity; latitude ~24°S)

Ephedra breana, *Adesmia* sp., *Bahia ambrosioides*, *Chuquiraga ulicina*, *Cristaria* sp., *Echinopsis coquimbana*, *E. spinibarbis*, *Euphorbia lactiflua*, *Gypothamnium pinifolium*, *Heliotropium philippianum*, *H. pycnophyllum*, *Lycium leiostemum*, *Nolina* sp., *Ophryosporus triangularis*, *Oxalis gigantea*, *Polyachyrus* sp., *Proustia cinerea*, *Salvia gilliesii*.

Shrubland/Chaparral–Woodland–Savanna

Serena–La Ligua (latitude 30°S, MAP 50–300 mm)

Adesmia sp., *Alstroemeria pelegrina*, *Aristolochia chilensis*, *Fuchsia lycioides*, *Haplopappus foliosus*, *Loasa urmenetae*, *Pouteria splendens*, *Schizanthus* sp.

Central zone (32°–37°S)

Acacia caven, *Jubaea chilensis*, *Lapageria rosea* (national flower of Chile), *Lithrea caustica*, *Mutisia* sp., *Nothofagus alessandri*, *N. glauca*, *Peumus boldus*, *Puya chilensis*, *Quillaja saponaria*, *Tropaeolum tricolor.*

Lower to Upper Montane Broad-Leaved Forest

Vegetación de lomas y de los bosques de neblina (slope and cloud forest)

Fern: *Hymenophyllum peltatum.* Angiosperms: *Copiapoa* sp., *Croton chilensis*, *Drimys winteri*, *Griselinia scandens*, *Mitraria coccinea*, *Peperomia coquimbensis*, *Salvia paposana*, *Tillandsia geissei*, *T. tragophoba.*

Los Andes de la Zona Central

Alstroemeria sp., *Berberis empetrifolia*, *Calandrinia* sp., *Calceolaria arachnoidea*, *C. corymbosa*, *C. hypericina*, *Chaetanthera* sp., *Haplopappus* sp., *Loasa* sp., *Maihuenia poeppigii*, *Nassauvia* sp., *Nastanthus agglomeratus*, *Nothofagus antarctica*, *N. dombeyi*, *N. obliqua*, *Oxalis enneaphylla*, *Schizanthus grahamii*, *S. hookeri*, *Senecio* sp., *Viola cotyledon.*

Bosques de *Araucaria*

Araucaria araucana.

Bosque lluvioso siempreverde
([temperate] rain forest; MAP ~1000 mm)

Ferns: *Adiantum chilense*, *Blechnum chilense*, *Hymenophyllum* sp., *Hypolepis poeppigii*, *Lophosoria quadripinnata*, *Megalastrum spectabile.* Gymnosperms: *Austrocedrus chilensis*, *Fitzroya cupressoides*, *Podocarpus nubigenus*, *P. salignus.* Angiosperms: *Boquila trifoliolata*, *Campsidium valdivianum*, *Chusquea parviflora*, *C. quila*, *Cissus striata*, *Drimys winteri*, *Escallonia rosea*, *E. rubra*, *Eucryphia cordifolia*, *Fascicularia* sp., *Fuchsia magellanica*, *Gevuina avellana*, *Gunnera tinctoria*, *Lapageria rosea*, *Lardizabala biternata*, *Laurelia sempervirens*, *Laureliopsis philippiana*, *Luzuriaga radicans*, *Myrceugenia* sp., *Persea lingue*, *Pilgerodendron uviferum*, *Proustia pyrifolia*, *Sarmienta scandens*, *Saxegothaea conspicua*, *Ugni molinae.*

Patagonia

Gymnosperm: *Austrocedrus chilensis.* Angiosperms: *Azorella* sp., *Baccharis magellanica*, *B. patagonica*, *Berberis empetrifolia*, *B. microphylla*, *Bolax* sp., *Chiliotrichum diffusum*, *Escallonia serrata*, *Festuca gracillima*, *Gaultheria pumila*, *Gunnera magellanica*, *Junellia tridens*, *Mulinum spinosum*, *Nothofagus antarctica*, *N. pumilio*, *Pilgerodendron uviferum.*

Tundra

Chile Antártico

Two vascular plants: *Deschampsia antarctica*, *Colobanthus quitensis.*

Alpine Tundra (Páramo, Puna)

El Altiplano o puna

~1900–3600 m

Baccharis boliviensis, *Mentzelia ignea*, *Trixis cacalioides*, *Viguera pazensis.*

3600–4000 m

Baccharis boliviensis, *Fabiana denudata*, *Parastrephia quadrangularis*, *Senecio nutans.*

Above 4000 m

Azorella compacta, *Polylepis tarapacana*, *Pycnophyllum molle.*

APPENDIX 1.23

Vegetation types of Argentina, with representative species, and plant formations used here indicated in parentheses. After Cabrera (1971, 1976) and various sources.

Region Neotropical

Dominio Amazónico (highest species diversity)

1. Provincia de las Yungas [montane broad-leaved forest, selva nublada (cloud forest), yungas–wet, mostly densely forested eastern slopes of the Andes Mountains], 500–2500 m, MAP 900–2500 mm, MAT 14°–26° C

Districto de las selvas de transición—*Acacia aroma* (edaphically dry), *Acrocomia chunta*, *Allophylus edulis*, *Amburana cearensis*, *Anadenanthera macrocarpa*, *Astronium urundeuva*, *Bombax argentinum*, *Buddleja albotomentosa*, *Calycophyllum multiflorum*, *Cassia carnaval*, *Cedrela angustifolia*, *Celtis pubescens*, *Chlorophora tinctoria*, *Chorisia insignis*, *Cnicothamnus lorentzii*, *Cordia trichotoma*, *Cupania vernalis*, *Enterolobium contortisiliquum*, *Eugenia uniflora*, *Gleditsia amorphoides*, *Ilex argentina*, *Lonchocarpus lilloi*, *Muntingia calabura*, *Myroxylon peruiferum*, *Parapiptadenia excelsa*, *Patagonula americana*, *Phyllostylon rhamnoides*, *Pisonia zapallo*, *Pithecellobium scalare*, *Pogonopus tubulosus*, *Pterogyne nitens*, *Ruprechtia laxiflora*, *Salix humboldtiana*, *Tabebuia avellanedae*, *Terminalia triflora*, *Tessaria integrifolia*, *Tipuana tipu*, *Trichilia hieronymi*, *Vernonia fulta.*

Distrito de las selvas montanas—Ferns and allied groups: *Lycopodium* sp., *Selaginella nova-hollandiae*, *Equisetum bogotense*, *Blechnum sprucei*, *Pteris deflexa*. Angiosperms: *Aechmea distichantha*, *Baccharis tucumanensis*, *Begonia boliviensis*, *B. micranthera*, *Blepharocalyx gigantea*, *Bocconia pearcei*, *Boehmeria caudata*, *Bomarea macrocephala*, *Cedrela angustifolia*, *C. lilloi*, *Cestrum lorentzianum*, *Chusquea lorentziana*, *Crinodendron tucumanum*, *Cupania vernalis*, *Doxantha unguis-cati*, *Elephantopus mollis*, *Enterolobium contortisiliquum*, *Epidendrum argentinense*, *Eugenia mato*, *E. pungens*, *Fagara coco*, *Hydrocotyle bonplandii*, *Ilex argentina*, *Iresine paniculata*, *Juglans australis*, *Malaxis padilliana*, *Mandevillea laxa*, *Manettia jorgensenii*, *Miconia ioneura*, *Oncidium viperinum*, *Oplismenus hirtellus*, *Parapiptadenia excelsa*, *Passiflora morifolia*, *P. tenuifila*, *P. urnifolia*, *Pavonia malvacea*, *Pennisetum latifolium*, *Pharus glaber*, *Phoebe porphyria*, *Piper tucumanum*, *Polymnia connata*, *Prunus tucumanensis*, *Pseudocaryophyllus guili*, *Rhipsalis* sp., *Seemannia gymnostoma*, *Senecio peregrinus*, *Sibthorpia conspicua*, *Stellaria media*, *Tabebuia avellanedae*, *Tibouchina paratropica*, *Tillandsia maxima*, *T. schreiteri*, *Urera baccifera*, *Vriesea friburgensis*.

Distrito de los bosques montanos—Gymnosperm: *Podocarpus parlatorei* (1000–1700 m). Angiosperms: *Alnus jorullensis* (1400–2100 m), *Amicia medicaginea*, *Baccharis* sp., *Bidens andicola*, *Calceolaria teucrioides*, *Duranta serratifolia*, *Gentianella* sp., Gramineae (*Chloris distichophylla*, *Deyeuxia polygama*, *D. rosea*, *Festuca hieronymi*, *Lamprothyrsus hieronymi*, *Paspalum lineispatha*), *Lippia turnerifolia*, *Polygala* sp., *Polylepis australis* (1900–2300 m), *Salvia* sp., *Sambucus peruviana*, *Schinus gracilipes*, *Stevia* sp., *Tagetes* sp.

2. Provincia Paranense, ~1000 m, MAP 1564–2012 mm, MAT 20°–21° C

Distrito de las selvas mixtas (montane broad-leaved forest, drier parts transition to shrubland/chaparral–woodland–savanna)—Ferns: *Alsophila atrovirens*, *A. procera*, *Dicksonia sellowiana*, *Hemitelia setosa*. Gymnosperm: *Araucaria angustifolia*. Angiosperms: *Allophylus edulis*, *Apuleia leiocarpa*, *Aspidosperma polyneuron*, *Astronium balansae*, *Balfourodendron riedelianum*, *Bastardiopsis densiflora*, *Cabralea oblongifoliola*, *Casearia sylvestris*, *Cecropia adenopus*, *Cedrela fissilis*, *Chrysophyllum gonocarpum*, *Chusquea uruguayensis*, *Citharexylum montevidense*, *Cordia trichotoma*, *Cordyline dracaenoides*, *Diatenopteryx sorbifolia*, *Erythrina crista-galli*, *Euterpe edulis*, *Ficus anthelminthica*, *F. guaranitica*, *F. monckii*, *Guadua trinii*, *Holocalyx balansae*, *Ilex paraguariensis*, *Inga uruguensis*, *Lonchocarpus leucanthus*, *Merostachys claussenii*, *Mimosa bimucronata*, *Myrocarpus frondosus*, *Nectandra lanceolata*, *N. saligna*, *Ocotea acutifolia*, *Olyra latifolia*, *Parapiptadenia rigida*, *Pharus glaber*, *Philodendron bipinnatifidum*, *Piper* sp., *Pouteria gardneriana*, *Prunus subcoriacea*, *Salix humboldtiana*, *Sapium haematospermum*, *S. longifolium*, *Solanum auriculatum*, *Syagrus romanzoffiana*, *Tabebuia ipe*, *T. pulcherrima*, *Urera baccifera*.

Distrito de los campos (grasslands, savannas)—*Andropogon lateralis*, *Aristida jubata*, *Axonopus compressus*, *Cyrtopodium punctatum*, *Elionurus muticus*, *E. tripsacoides*, *Eragrostis rojasii*, *Mayaca fluviatilis*, *M. sellowiana*, *Panicum bergii*, *P. prionitis*, *Paspalum haumanii*, *P. guaraniticum*, *P. notatum*, *P. urvillei*.

Dominio Chaqueño

3. Provincia Chaqueña [mostly dry shrubland/chaparral–woodland–savanna or bosque xerófilo caducifolio, chaco, some inundated areas (freshwater herbaceous bog/marsh/swamp), aquatics], MAP 500 (west)–1200 mm (east), MAT 20°–23° C

Distrito Chaqueño oriental—Aquatics (*Cabomba australis*, *Ceratophyllum demersum*, *Eichhornia azurea*, *E. crassipes*, *Myriophyllum brasiliense*, *Pontederia lanceolata*, *Potamogeton* sp., *Reussia subovata*, *Sagittaria montevidensis*, *Thalia multiflora*, *Utricularia* sp., *Victoria cruziana*), inundated areas (*Cyperus giganteus*, *Eriocaulon magnun*, *Fuirena robusta*, *Scirpus cubensis*, *Typha latifolia*), *Acacia caven*, *A. praecox*, *Acanthosyris falcata*, *Aechmea distichantha*, *Aloysia gratissima*, *Aspidosperma quebracho-blanco*, *Astronium balansae*, *Bromelia serra*, *Bumelia obtusifolia*, *Caesalpinia paraguariensis*, *Castela coccinea*, *Celtis spinosa*, *Cereus cavendishii*, *Cleistocactus baumannii*, *Copernicia australis*, *Cyperus giganteus* (inundated areas), *Diplokeleba floribunda*, *Dyckia ferox*, *Elionurus muticus*, *Eriocereus guelichii*, *E. martini*, *Geoffroea decorticans*, *Gleditsia amorphoides*, *Leptochloa virgata*, *Melica argyrea*, *Opuntia retrorsa*, *Parkinsonia aculeata*, *Paspalum inaequivalve*, *P. unispicatum*, *Patagonula americana*, *Phyllostylon rhamnoides*, *Pisonia zapallo*, *Pithecellobium scalare*, *Prosopis alba*, *P. kuntzei*, *P. nigra*, *P. ruscifolia*, *Ruprechtia laxiflora*, *Schinopsis balansae*, *Tabebuia ipe*, *T. nodosa*, *Ziziphus mistol*.

Distrito Chaqueño occidental—*Acacia aroma*, *A. caven*, *A. furcatispina*, *Allenrolfea patagonica*, *Aspidosperma quebracho-blanco*, *Atamisquea emarginata*, *Bougainvillea infesta*, *B. praecox*, *Bromelia hieronymi*, *B. serra*, *Bulnesia bonariensis*, *B. foliosa*, *B. sarmientoi*, *Caesalpinia paraguariensis*, *Capparis tweediana*, *Celtis chichape*, *Cercidium praecox*, *Cereus coryne*, *C. validus*, *Chorisia insignis*, *Copernicia australis*, *Deinacanthon urbanianum*, *Digitaria sanguinalis*, *Gouinia latifolia*, *Heterostachys ritteriana*, *Maytenus spinosa*, *Mimosa detinens*, *Opuntia quimilo*, *Pennisetum frutescens*, *Pereskia sacharosa*, *Prosopis kuntzei*, *P. nigra*, *Quiabentia chacoensis*, *Ruprechtia apetala*, *R. triflora*, *Salix humboldtiana*, *Schinopsis balansae*, *S. lorentzii*, *Setaria argentina*, *S. gracilis*, *Tessaria integrifolia*, *Trichloris crinita*, *Trithrinax biflabellata*, *Ziziphus mistol*.

Distrito Chaqueño Serrano—*Acacia caven*, *A. visco*, *Aspidosperma quebracho-blanco*, *Celtis chichape*, *Chorisia insignis*, *Fagara coco*, *Jodina rhombifolia*, *Lithraea ternifolia*, *Phoradendron* sp., *Phrygilanthus* sp., *Prosopis torquata*, *Psittacanthus* sp., *Ruprechtia apetala*, *Schinopsis haenkeana*, *Schinus areira*. Highest altitudes (Sierra Grandes de Córdoba): *Polylepis australis*, *Festuca* sp., *Stipa* sp.

Distrito de las Sabanas (savanna)—*Bothriochloa barbinodis*, *Elionurus muticus*, *Leptochloa chloridiformis*, *Leptocoryphium lanatum*, *Schizachyrium paniculatum*, *Sorghastrum pellitum*, *Spartina argentinensis*.

4. Provincia del Espinal (shrubland/chaparral), MAP 340–1170 mm, MAT 15°–20° C

Distrito del Ñandubay—*Acacia caven*, *Allophylus edulis*, *Andropogon lateralis*, *Aristida* sp., *Aspidosperma quebracho-blanco*, *Axonopus* sp., *Bothriochloa laguroides*, *Briza* sp., *Bumelia obtusifolia*, *Cassia*

corymbosa, *Castela tweedii*, *Celtis spinosa*, *C. tala*, *Elionurus muticus*, *Eugenia uniflora*, *Fagara hyemalis*, *Geoffroea decorticans*, *Gochnatia argentina*, *Jodina rhombifolia*, *Melica macra*, *Panicum racemosum*, *Passiflora coerulea*, *Paspalum* sp., *Pithecoctenium cynanchoides*, *Prosopis algarobilla* (ñandubay), *P. nigra*, *Rollinia emarginata*, *Schinus longifolia*, *S. molle*, *Scutia buxifolia*, *Setaria caespitosa*, *Smilax campestris*, *Stipa* sp., *Syagrus yatay*, *Tabebuia nodosa*, *Tabernaemontana australis*, *Trithrinax campestris*.

Distrito del Algarrobo (extensively cultivated)—*Celtis spinosa*, *Geoffroea decorticans*, *Propopis alba*, *P. nigra*.

Distrito del Caldén—Gymnosperms: *Ephedra ochreata*, *E. triandra*. Angiosperms: *Allenrolfea patagonica*, *Atamisquea emarginata*, *Baccharis artemisioides*, *B. ulicina*, *Cassia aphylla*, *Condalia microphylla*, *Cyclolepis genistoides*, *Elionurus muticus*, *Geoffroea decorticans*, *Heterostachys olivascens*, *H. ritteriana*, *Hyalis argentea*, *Jodina rhombifolia*, *Larrea divaricata*, *Lycium chilense*, *Panicum urvilleanum*, *Piptochaetium napostaense*, *Poa lanuginosa*, *P. ligularis*, *Prosopanche americana*, *Prosopidastrum globosum*, *Prosopis alpataco*, *P. caldenia*, *P. flexuosa*, *P. nigra*, *Schinus fasciculatus*, *Schizachyrium* sp., *Setaria globulifera*, *S. mendocina*, *Sporobolus rigens*, *Stipa clarazii*, *S. gynerioides*, *S. tenuis*, *S. tenuissima*, *Trichloris crinita*, *Ximenia americana*.

5. Provincia Prepuneña (high-altitude dry phase of the montane broad-leaved forest, estepa arbustiva xerófila; transition between yungas and puna, chaco and puna, or monte and puna), 2000–3400 m

Ferns and allied groups: *Pellaea nivea*, *P. ternifolia*, *Selaginella peruviana*. Angiosperms: *Abromeitiella brevifolia*, *Adesmia inflexa*, *Agrostis nana*, *Aphyllocladus spartioides*, *Baccharis salicifolia*, *Bougainvillea spinosa*, *Bulnesia schickendantzii*, *Caesalpinia trichocarpa*, *Cassia crassiramea*, *Cercidium andicola*, *Chuquiraga erinacea*, *Cylindropuntia* sp., *Deuterocohnia strobilifera*, *Digitaria californica*, *Echeveria peruviana*, *Gochnatia glutinosa*, *Junellia juniperina*, *Justicia pauciflora*, *Krameria iluca*, *Lobivia* sp., *Lycium ciliatum*, *L. venturii*, *Munroa argentina*, *Opuntia* sp., *Parodia maassii*, *Prosopis ferox*, *Proustia cuneifolia*, *Psila boliviensis*, *Puya dyckioides*, *P. fiebrigii*, *Schinus areira*, *Stipa leptostachya*, *Tephrocactus* sp., *Tillandsia gilliesii*, *T. pusilla*, *Trichocereus pasacana*, *T. poco*, *Zuccagnia punctata*.

6. Provincia del Monte [desert to shrubland/chaparral–woodland–savanna; matorral o la estepa arbustiva xerófila, sammófila (dune) o halófila; climax community jarillal (jarillas = *Larrea*)], MAP 80–250 mm, MAT 13°–17.5° C

Acacia aroma, *Allenrolfea vaginata*, *Bougainvillea spinosa*, *Bulnesia retama*, *B. schickendantzii*, *Caesalpinia punctata*, *Cassia aphylla*, *C. rigida*, *Cercidium praecox*, *Chuquiraga erinacea*, *Flourensia polyclada*, *Gochnatia glutinosa*, *Hyalis argentea*, *Larrea cuneifolia*, *L. divaricata*, *L. nitida*, *Mimosa ephedroides*, *Monttea aphylla*, *Plectrocarpa rougesii*, *P. tetracantha*, *Prosopidastrum globosum*, *Prosopis alpataco*, *P. chilensis*, *P. flexuosa*, *P. torquata*, *Proustia cuneata*, *Sporobolus maximus*, *S. rigens*, *Suaeda divaricata*, *Zuccagnia punctata*.

7. Provincia Pampeana (grassland, pampas), plains to 1200 m, MAP 600–1100 mm, MAT 13°– 17° C

Ferns: *Anemia tomentosa*, *Polystichum mohrioides*. Angiosperms: *Acacia bonariensis*, *A. caven*, *Adesmia pampeana*, *Allophylus edulis*, *Anemone decapetala*, *Aster* sp., *Baccharis articulata*, *B. cordifolia*, *B. notosergila*, *B. tandilensis*, *B. trimera*, *B. ulicina*, *Berroa* sp., *Blepharocalyx tweediei*, *Carduus acanthoides*, *Cassia corymbosa*, *Celtis spinosa*, *Cestrum corymbosum*, *Chaptalia* sp., *Colletia paradoxa*, *C. spinosissima*, *Convolvulus hermanniae*, *Conyza chilensis*, *Cynara cardunculus*, *Discaria longispina*, *Distichlis scoparia*, *D. spicata*, *Dodonaea viscosa*, *Eryngium eburneum*, *Eupatorium buniifolium*, *Fagara hyemalis*, *Gaultheria phillyreafolia*, *Gavilea odoratissima*, *Glandularia peruviana*, Gramineae (*Agrostis montevidensis*, *Aristida murina*, *A. pallens*, *Avena barbata*, *Bothriochloa laguroides*, *Bouteloua megapotamica*, *Briza brizoides*, *B. minor*, *B. subaristata*, *Bromus brevis*, *B. unioloides*, *Danthonia montevidensis*, *Elionurus muticus*, *Eragrostis cilianensis*, *E. lugens*, *Festuca pampeana*, *F. ventanicola*, *Hordeum pusillum*, *Melica bonariensis*, *M. brasiliana*, *M. macra*, *Panicum bergii*, *P. milioides*, *P. racemosum*, *P. urvilleanum*, *Paspalum notatum*, *P. plicatulum*, *P. quadrifarium*, *P. vaginatum*, *Piptochaetium bicolor*, *P. chaetophorum*, *P. leiopodum*, *P. montevidense*, *P. napostaense*, *Poa annua*, *P. bonariensis*, *P. lanigera*, *P. lanuginosa*, *P. ligularis*, *Sorghastrum pellitum*, *Spartina densiflora*, *Stipa ambigua*, *S. caudata*, *S. charruana*, *S. clarazii*, *S. filiculmis*, *S. juncoides*, *S. neesiana*, *S. pampeana*, *S. papposa* [*S. delilei*], *S. poeppigiana*, *S. tenuis*, *S. tenuissima*, *S. trichotoma*, *S. ventanicola*), *Grindelia* sp., *Heimia salicifolia*, *Hypochaeris radicata*, *Jodina rhombifolia*, *Lathyrus nervosus*, *Margyricarpus pinnatus*, *Medicago minima*, *M. polymorpha*, *Micropsis* sp., *Mimosa rocae*, *Mulinum spinosum*, *Nectandra falcifolia*, *Ocotea acutifolia*, *Oxalis cordobensis*, *O. macachin*, *Petunia axillaris*, *Phytolacca dioica*, *Plantago bismarckii*, *Polygala linoides*, *Pouteria salicifolia*, *Prosopidastrum globosum*, *Prosopis alba*, *Salicornia ambigua* (halophyte), *Sambucus australis*, *Sapium haematospermum*, *Schinus longifolius*, *Scirpus californicus*, *Scutia buxifolia*, *Sebastiania brasiliensis*, *Senecio ventanensis*, *Sesuvium portulacastrum* (halophyte), *Sphaeralcea* sp., *Thelesperma megapotamicum*, *Trifolium polymorphum*, *Vernonia rubricaulis*, *Vicia* sp., *Wedelia buphthalmiflora*. Freshwater herbaceous bog/marsh/swamp: *Distichia* sp., *Hyalis argentea*, *Juncus acutus*, *Paspalum quadrifarium*, *Scirpus californicus*, *S. giganteus*, *Solanum malacoxylon*, *Spartina densiflora*, *Typha* sp., *Zizaniopsis bonariensis*. Aquatic: *Azolla filiculoides* (floating fern). Beach/strand/dune: *Adesmia incana*, *Panicum racemosum*, *Spartina ciliata*.

Dominio Andino–Patagónico (highest endemism)

8. Provincia Altoandina (páramo at highest elevations), sea level–4400 m, MAT to –1.5° C at Cristo Redentor, Province of Mendoza at 3829 m

Gymnosperm: *Ephedra andina*. Angiosperms: *Adesmia caespitosa*, *A. glanduligera*, *A. nanolignea*, *A. obovata*, *A. patancana*, *A. pinifolia*, *A. subterranea*, *A. uspallatenis*, *Andesia bisexualis*, *Artemisia copa*, *Aschersoniodoxa mandoniana*, *Azorella compacta*, *Baccharis incarum*, *Berberis empetrifolia*, *Cajophora coronata*, *Calandrinia acaulis*, *Calceolaria glacialis*, *Carex incurva*, *Cortaderia pilosa*, *Deyeuxia* sp., *Distichia muscoides*, *Empetrum rubrum*, *Gentiana prostrata*, *Gentianella punensis*, Gramineae (*Agrostis glabra*, *Festuca chrysophylla*, *F. eriostoma*, *F. monticola*, *F. orthophylla*, *F. scirpifolia*, *F. weberbaueri*, *Hordeum secalinum*, *Poa gymnantha*, *P. holciformis*, *P. obvallata*, *Stipa chrysophylla*, *S. frigida*, *S. scirpea*, *S. speciosa*, *S. tenuissima*, *S. vagi-*

nata), *Hypsela oligophylla*, *Mulinum ovalleanum*, *Nassauvia lagascae*, *Nototriche anthemidifolia*, *Oxalis compacta*, *Oxychloe andina*, *Parodiodoxa chionophila*, *Perezia ciliosa*, *Plantago barbata*, *Pycnophyllum molle*, *Scirpus atacamensis*, *Senecio algens*, *S. breviscapus*, *S. graveolens*, *S. uspallatensis*, *S. viridis*, *Silene* sp., *Tropaeolum polyphyllum*, *Valeriana spathulata*, *Werneria poposa*, *W. pygmaea*.

9. Provincia Puneña (páramo, puna, estepa arbustiva), 3400–4500 m, to 2000 m along the coasts, MAP 103–324 mm, MAT 7.5°–9.9° C

Gymnosperm: *Ephedra breana*. Angiosperms: *Acantholippia hastulata*, *Adesmia horridiuscula*, *A. spinosissima*, *Astragalus bustillosii*, *Baccharis incarum*, *Fabiana densa*, Gramineae (*Bouteloua simplex*, *Festuca scirpifolia*, *Muhlenbergia fastigiata*, *Panicum chloroleucum*, *Sporobolus rigens*), *Hypsela oligophylla*, *Ipomoea minuta*, *Juncus depauperatus*, *Junellia seriphioides*, *Lampaya castellani*, *Nardophyllum armatum*, *Oputia soehrensii*, *Oreocereus celsianus*, *O. trollii*, *Parastrephia lepidophylla*, *P. phyliciformis*, *Pennisetum chilense*, *Plantago tubulosa*, *Polylepis tomentella*, *Prosopis ferox*, *Psila boliviensis*, *Scirpus atacamensis*, *Senecio viridis*, *Tetraglochin cristatum*, *Trichocereus pasacana*, *T. poco*, *Trifolium amabile*.

10. Provincia Patagónica (low woodland, estepa arbustiva), MAP 100–500 mm, MAT 5°–13.4° C

Gymnosperm: *Ephedra ochreata*. Angiosperms: *Acaena pinnatifida*, *Adesmia campestris*, *Ameghinoa patagonica*, *Anarthrophyllum rigidum*, *Atriplex lampa*, *A. reichii*, *Benthamiella patagonica*, *Berberis cuneata*, *Brachyclados caespitosus*, *Calceolaria polyrrhiza*, *Cerastium arvense*, *Chuquiraga avellanedae*, *C. rosulata*, *Colliguaya* sp., *Distichlis scoparia*, *D. spicata*, Gramineae (*Agropyron fuegianum*, *Agrostis leptotricha*, *Bromus macrantherus*, *Danthonia collina*, *Deschampsia flexuosa*, *Elymus antarcticus*, *E. patagonicus*, *Festuca argentina*, *F. gracillima*, *F. pallescens*, *F. pyrogea*, *Hordeum comosum*, *Poa atropidiformis*, *P. huecu*, *P. ligularis*, *Stipa humilis*, *S. neaei*, *S. speciosa*), *Grindelia chiloensis*, *Juncus lesueurii*, *Junellia seriphioides*, *J. tridens*, *Larrea ameghinoi*, *Lepidophyllum cupressiforme*, *Loasa bergii*, *Lycium chilense*, *Magallana porifolia*, *Mulinum spinosum*, *Mutisia retrorsa*, *Nardophyllum obtusifolium*, *Nassauvia axillaris*, *N. glomerulosa*, *Phacelia magellanica*, *Plantago maritima*, *Pleurophora patagonica*, *Scirpus californicus*, *Senecio bracteolatus*, *S. filaginoides*, *S. patagonicus*, *Trevoa patagonica*, *Tristagma patagonicum*, *Viola maculata*.

Dominio Subantártico (see Morrone, 2000, for delimitation)

11. Provincia Subantártica (woodland, bosque caducifolio o perennifolio), MAP 700–2000 mm, MAT 5.4°–9.5° C

Musci: *Sphagnum magellanicum*. Ferns and allied groups: *Equisetum bogotense*, *Blechnum chilense*, *B. penna-marina*, *Lophosoria quadripinnata*, *Polystichum mohrioides*. Gymnosperms: *Araucaria araucana*, *Austrocedrus chilensis*, *Fitzroya cupressoides*, *Pilgerodendron uviferum*, *Podocarpus nubigenus*, *Saxegothea conspicua*. Angiosperms: *Acaena pinnatifida*, *Adenocaulon chilense*, *Aextoxicon punctatum*, *Alstroemeria aurantiaca*, *Aristolelia macqui*, *Azara microphylla*, *Berberis buxifolia*, *B. darwinii*, *Chacaya* sp., *Chloraea alpina*, *Codonorchis lessonii*, *Cortaderia pilosa*, *Dasyphyllum diacanthoides*, *Desfontainia spinosa*, *Drimys winteri*, *Embothrium coccineum*, *Escallonia virgata*, *Eucryphia cordifolia*, *Fabiana imbricata*, *Fuchsia magellanica*, *Gevuina avellana*, Gramineae (*Chusquea argentina*, *C. culeou*, *Poa flabellata*), *Gunnera chilensis*, *Lathyrus magellanicus*, *Laurelia philippiana*, *Leuceria thermarum*, *Loasa argentina*, *Lomatia ferruginea*, *L. hirsuta*, *Maytenus boaria*, *M. disticha*, *M. magellanica*, *Mutisia decurrens*, *M. spinosa*, *Myrceugenella apiculata*, *Myzodendrum* sp., *Nardophyllum obtusifolium*, *Nothofagus antarctica*, *N. betuloides*, *N. dombeyi*, *N. obliqua*, *N. procera*, *N. pumilio*, *Perezia palustris*, *Pernettya mucronata*, *Persea lingue*, *Rhaphithamnus* sp., *Ribes magellanicum*, *Schinus patagonicus*, *Scirpus californicus*, *Senecio candicans*, *S. parodii*, *Ugni molinae*, *Weinmannia trichosperma*.

12. Provincia Insular (tundra)

Ferns and allied groups: *Lycopodium magellanicum*, *Blechnum magellanicum*. Angiosperms: *Acaena microcephala*, *Astelia pumila*, *Azorella lycopodioides*, *Baccharis magellanica*, *Bolax gummifera*, *Carex trifida*, *Chiliotrichum diffusum*, *Drapetes muscosus*, *Empetrum rubrum*, Gramineae (*Cortaderia pilosa*, *Deschampsia flexuosa*, *Poa antarctica*, *P. flabellata*), *Gunnera magellanica*, *Hebe elliptica*, *Luzula alopecurus*, *Pernettya pumila*, *Rostkovia magellanica*, *Senecio candicans*, *S. littoralis*.

Dominio Antártico

13. Provincia Antártica (tundra)

Musci: *Andreaea depressinervis*, *Brachythecium antarcticum*, *Hypnum* (*Calliergon*) *sarmentosum*, *Pogonatum alpinum*, *Tortula excelsa*. Lichens: *Cladonia coccifera*, *C. pyxidata*, *Neuropogon melaxanthum*. Angiosperms: *Colobanthus quitensis*, Gramineae (*Deschampsia elegantula*).

APPENDIX 1.24

Vegetation types of Guyana and French Guiana with representative species. After Granville (1988, 2002, lettered and numbered subdivisions slightly modified). For other rain forest trees see text (Chapter 3, Guianas).

Guyana

Upland moist forests (lowland moist forest, Prance, 1979; rain forest, Fanshawe, 1952)

Upland moist forest on ferrallitic soil (sea level to 600 m, MAP >2000 mm; lowland, moist, high species diversity)

Upland moist forest on lateritic crusts (hilltops in the lowlands, upland slopes, less species diversity)

Montane and lower montane moist forests

Lower montane moist forest (400–1300 m, fog common, bryophytes and vascular epiphytes common, cloud forest)

Montane moist forest (1200–1600 m; slopes of tepuis, Mt. Roraima)

Inundated forests

Permanent swamp forest (Prance, 1979, 1989; swamp forest [Beard, 1944; Fanshawe, 1952; Lindeman, 1953])—*Euterpe oleracea*, *Mauritia flexuosa*, *Mora excelsa*, *Triplaris surinamensis*

Periodically flooded forest (Prance, 1979, 1989; marsh forest [Lindeman, 1953])—*Symphonia globulifera*, *Virola surinamensis*

Mangrove forests

Coastal mangrove—*Avicennia nitida*

Estuary mangrove—*Rhizophora mangle*

Tidal swamp forest

Seasonal swamp forest

Gallery forest (along rivers in the Roraima–Rupununi savannas)—*Mauritia flexuosa*

Transition forests (Prance, 1979, 1989, transition between rain forest and open areas; seasonal forests [Beard, 1944; Fanshawe, 1952])

Evergreen seasonal forest

Semi-evergreen seasonal forest (Fanshawe, 1952; dry forest [Prance, 1979, 1989])

Forest on white sand soils (Prance, 1979, 1989; dry evergreen forest [Beard, 1944; Fanshawe, 1952]); savanna forest (Lindeman, 1953), beaches, leached sandstones

Wallaba forest—*Eperua falcata*, *E. rubiginosa*

Xeromorphic rain forest, woodland and scrub (woodland and scrub = savanna forest; Lindeman, 1953)—*Clusia fockeana*, *C. nemorosa*, *Humiri balsamifera*, *H. floribunda*

French Guiana

I. La végétation des terres basses (alluvions marines)

A. Végétation de la plaine côtière récente

1. Mangroves

Mangrove côtière récente—*Avicennia germinans*, *Laguncularia racemosa*

Mangrove d'estuaire—*Mauritia flexuosa*, *Montrichardia arborescens*, *Pterocarpus officinalis*, *Rhizophora mangle*

2. Plages et rochers du littoral—*Acrocomia aculeata*, *Canavalia maritima*, *Cereus hexagonus*, *Furcraea foetida*, *Ipomoea pes-caprae*

3. Marais subcôtièrs—Ferns: *Blechnum serrulatum*, *Thelypteris interrupta*. Angiosperms: *Chrysobalanus icaco*, *Cyperus giganteus*, *Echinochloa polystachya*, *Eleocharis mutata*, *Lagenocarpus guianensis*, *Rhynchospora corymbosa*, *Scleria* sp., *Typha latifolia*

4. Forêts marécageuses—*Euterpe oleracea*, *Ischnosiphon obliquus*, *Symphonia globulifera*, *Virola surinamensis*

5. Anciens cordons littoraux (cheniers)—*Astrocaryum vulgare*, *Hymenaea courbaril*, *Protium heptaphyllum*

B. Végétation de la plaine côtière ancienne

1. Forêts sur flats—*Maximiliana maripa*, *Phenakospermum guianensis*

2. Savanes côtières—*Byrsonima verbascifolia*, *Clidemia rubra*, *Curatella americana*, *Heliconia psittacorum*, *Phenakospermum guianensis*, *Rhynchanthera grandiflora*

C. Végétation des sables détritiques continentaux (white sand forests)—*Clusia fockeana*, *C. nemorosa*, *Humiria floribunda*, *Myrica sylvatica*

II. La végétation des terres hautes (collines du socle Précambrien)

A. Seuils rocheux des rivières ("sauts")—*Mourera fluviatilis*

B. Forêts de basses altitude (0–500 m)

1. Forêts hautes sur sols hydromorphes

Forêts marécageuses de l'intérieur

Forêts ripicoles—*Eperua falcata*, *Inga* sp., *Pachira aquatica*, *Posoqueria longiflora*, *Triplaris weigeltiana*

Forêts inondables d'îlots de "sauts"—Fern: *Adiantum latifolium*. Angiosperm: *Scleria secans*

Forêts de flat des vallées alluviales

2. Forêts hautes sur sols drainés—*Andira* sp., *Aniba rosaeodora*, *Apeiba* sp., *Aspidosperma* sp., *Astrocaryum paramaca*, *A. sciophilum*, *Bactris* sp., *Bauhinia* sp., *Calathea* sp., *Chimarrhis turbinata*, *Clidemia* sp., *Couratari* sp., *Coussarea* sp., *Davilla rugosa*, *Dicorynia guianensis*, *Diplotropis purpurea*, *Eschweilera* sp., *Faramea guianensis*, *Ficus nymphaeifolia*, *Geissospermum* sp., *Geonoma* sp., *Heliconia* sp., *Hymenolobium* sp., *Inga bourgoni*, *Ischnosiphon* sp., *Leandra* sp., *Lecythis zabucajo*, *Manilkara bidentata*, *Miconia* sp., *Monstera* sp., *Oenocarpus bacaba*, *Olyra* sp., *Pariana* sp., *Peltogyne venosa*, *Pharus* sp., *Philodendron* sp., *Psychotria* sp., *Socratea exorrhiza*, *Swartzia* sp., *Tanaecium nocturnum*, *Vouacapoua americana*, *Zygia racemosa*, *Z. tetragona*

C. Forêts de moyenne altitude (500–860 m)—Fern: *Cyathea* sp. Angiosperms: *Geonoma euspatha*, *G. umbraculiformis*, *Psychotria* sp.

D. Végétation des inselbergs (hills, flatlands rising from surrounding plains)—*Axonopus ramosus* (grass of wet depressions), *Cyrtopodium andersonii*, *Encyclia granitica*, *Ernestia* sp., *Irlbachia purpurescens*, *Ischaemum guianense*, *Pitcairnia geyskesii*. Aquatic: *Utricularia* sp. Isolated woods and forest margins: *Anthurium solitarium*, *Catopsis berteroniana*, *Clusia* sp., *Eriotheca surinamensis*, *Erythroxylum citrifolium*, *Eugenia biflora*, *Myrcia guianensis*, *M. saxatilis*

E. "Cambrouses" (dense, impenetrable, monospecific enclaves within the forest; viz., phases)—*Guadua macrostachya* (bamboo), *Lasiacis ligulata*

APPENDIX 1.25

Representative plants of the Brazilian cerrado. After Eiten (1972), Novaes Pinto (1994), and various sources.

Ferns: *Anemia* (several species, *A. elegans*, *A. fulva*, *A. hirsuta*). Angiosperms: *Acacia recurvata*, *Aegiphila lanata*, *Aeschynomene brasila*, *Agonandra brasiliensis*, *Alibertia concolor*, *Allagoptera campestris*, *Anacardium humile*, *Ananas ananassoides*, *Andira humilis*, *Annona crassiflora*, *Arrabidaea brachypoda* (many species), *Astrocaryum campestre*, *Attalea ceraennsis*, *Banisteriopsis adenopoda* (many species), *Bauhinia dumosa*, *Bowdichia virgilioides*, *Bromelia antiacantha*, *Brosimum gaudichaudii*, *Buchenavia tomentosa*, *Butia leiospatha*, *Byrsonima coccolobifolia*, *B. crassifolia*, *Byttneria scalpellata*, *Caliandra parviflora*, *Campomanesia corymbosa*, *Camptosema pedicellatum*, *Caryocar brasiliense*, *Casearia sylvestris*, *Cassia ferruginea*, *Chamaecrista basifolia* (many species), *Chromolaena cryptantha*, *Cissampelos ovalifolia*, *Cochlospermum regium*, *Cocos coronata*, *Combretum laxum*, *Connarus suberosus*, *Copaifera cordifolia*, *Copernicia prunifera*, *Cordia axillaris* (many species), *Crotalaria acutifolia*, *Croton adenodontus* (many species), *Curatella americana*, *Dalbergia violacea*, *Davilla elliptica*, *Declieuxia cordigera*, *Didymopanax macrocarpum*, *Dimorphandra mollis*, *Diospyros hispida*, *Dipteryx alata*, *Diptychandra glabra*, *Duguettia furfuracea*, *Enterolobium contortisiliquum*, *Eriosema congestum*, *Eriotheca gracilipes*, *Erythroxylum suberosum*, *Eugenia* sp. (many species), *Guazuma ulmifolia*, *Hancornia speciosa*, *Harpalyce brasiliana*, *Helicteres ovata*, *Heteropterys brasiliensis*, *Hirtella glandulosa*, *Hymenaea stignocarpa*, *Ilex affinis*, *Indigofera hirsuta*, *Inga affinis*, *Jacaranda decurens* (many species), *Kielmeyera rosea* (many species), *Krameria argentea*, *Lafoensia pacari*, *Lantana aristata*, *Lippia elegans* (many species), *Luehea* sp., *Machaerium aculeatum* (many species), *Magonia* sp., *Matayba* sp., *Miconia affinis* (many species), *Mikania acuminata*, *Myrcia capitata* (many species), *Nectandra cissiflora*, *Neea theifera*, *Ocotea aciphylla*, *Odontadenia hypoglauca*, *Orbignya barbosiana*, *Ouratea acuminata*, *Paepalanthus elongatus* (many species), *Palicourea rigida*, *Parinari obtusifolia*, *Peixotoa goiana*, *Phorodendron mucronatum* (many species), *Physocalymma scaberrimum*, *Piptocarpha rotundifolia*, *Plathymenia reticulata*, *Pouteria lateriflora*, *Protium brasiliense*, *Pseudobombax longiflorum*, *Psidium firmum*, *Psittacanthus robustus*, *Psychotria capitata* (many species), *Qualea grandiflora*, *Rapanea umbellata*, *Rhodocalyx rotundifolius*, *Roupala montana*, *Rudgea viburnoides*, *Ruellia asperula* (many species), *Salacia amygdalina*, *Salvertia convallariodora*, *Sapium marginatum*, *Sebastiania bidentata*, *Serjania erecta*, *Simarouba versicolor*, *Solanum crinitum* (many species), *Spiranthera odoratissima*, *Struthanthus* sp., *Strychnos pseudoquina*, *Stryphnodendron adstringens*, *Styrax camporum*, *Sweetia elegans*, *Syagrus comosa*, *Symplocos nitens*, *Tabebuia caraiba* (many species), *Terminalia argentea*, *Tetrapterys ambigua*, *Tibouchina stenocarpa*, *Tillandsia recurvata*, *Tocoyena formosa*, *Vellozia flavicans*, *Virola urbaniana*, *Vochysia elliptica*, *Waltheria communis*, *Wunderlichia crulsiana*, *Xylopia aromatica*, *Zeyheria digitali.*

Gramineae: *Andropogon bicornis*, *Aristida pallens*, *Axonopus pressus*, *Echinolaena inflexa*, *Eragrostis neesii*, *Gymnopogon doellii*, *Ichnanthus pallens*, *Panicum campestre* (many species), *Paspalum ammodes* (many species), *Setaria geniculata*, *Trachypogon mollis*, *Tristachya.* Cyperaceae: *Bulbostylis capillaris*, *Cyperus diffusus* (many species), *Dichromena ciliata*, *Fimbristylis capillaris*, *Rhynchospora albiceps* (many species), *Scleria latifolia.*

Herbs and forbs (ground cover plants): *Achyrocline alata*, *Baccharis camporum* (many species), *Bidens graveolens*, *Borreria peruviana*, *Calea cuneifolia*, *Camerea* sp., *Cuphea melvilla* (many species), *Dalechampia linearis*, *Diplusodon oblongus* (many species), *Dorstenia heringeri*, *Elephantopus biflorus*, *Eremanthus glomerulatus*, *Eryngium ebracteatum*, *Eupatorium amygdalinum*, *Euphorbia caecorum*, *Galactia glaucesecens*, *Hibiscus cucurbitaceus*, *Hyptis cana* (many species), *Ichthyothere integrifolia*, *Indigofera gracilis*, *Jatropha gossypiifolia*, *Julocroton humilis*, *Lupinus velutinus*, *Manihot anomala* (many species), *Marsypianthes montana*, *Microlicia fasciculata*, *Mimosa debilis* (many species), *Mitracarpus villosus*, *Oxalis ciliata*, *Pavonia cancellata*, *Peltaea acutifolia*, *Piriqueta selloi*, *Polygala* sp. (many species), *Porophyllum angustissimum*, *Rhabdocaulon denudatum*, *Richardia brasiliensis*, *Richeria australis*, *Salvia brevipes*, *Staelia capitata*, *Stevia collina*, *Turnera longiflora*, *Vernonia brevifolia* (many species), *Wedelia* sp.

Orchids: *Cleistes aphylla*, *Cyrtopodium pallidum* (many species), *Habenaria fastor* (many species).

Vines: *Aristolochia arcuata*, *Cissus erosa*, *Evolvulus lagopodioides*, *Ipomoea argentea* (many species), *Merremia aegyptia*, *Mimosa albolanata* (many species), *Passiflora alata* (many species), *Smilax brasiliensis.*

APPENDIX 1.26

Vegetation of the Pantanal with representative species. After Prance and Schaller (1982) and Por (1995).

Shrubland/Chaparral–Woodland–Savanna (cerrado, caatingas, chaco elements)

Acacia farnesiana, *Acosmium* sp., *Acrocomia* sp., *Aspidosperma pyrifolium*, *A. ulei*, *Astronium* cf. *lecointei*, *Bowdichia virgilioides*, *Bromelia* sp., *Buchenavia tomentosa*, *Bulnesia sarmientoi*, *Byrsonima coccolobifolia*, *Caesalpinia paraguariensis*, *Calliandra parviflora*, *Callisthene fasciculata*, *Calycophyllum multiflorum*, *Caryocar brasiliense*, *Cavanillesia* sp., *Ceiba pentandra*, *Cereus bonplandii*, *C. peruvianus*,

Combretum lanceolatum, *C. leprosum*, *Copaifera chodatiana*, *Copernicia alba*, *Cordia glabrata*, *Curatella americana*, *Diptychandra glabra*, *Enterolobium contortisiliquum*, *Hymenaea courbaril* (transition to Amazonia semi-deciduous forest), *H. stigonocarpa*, *Jatropha phyllacantha*, *Kielmeyera coriacea*, *Lafoensia pacari*, *L. punicifolia*, *Magonia* sp., *Monvillea cavendishii*, *Odontadenia hypoglauca*, *Opuntia stenarthra*, *Pereskia sacharosa*, *Phyllostylon* sp., *Piptadenia macrocarpa*, *Pouteria* sp., *Prosopis* sp., *Pseudobombax marginatum*, *Pterogyne nitens*, *Qualea grandiflora*, *Q. parviflora*, *Rhodocalyx rotundifolius*, *Schinopsis quebracho-colorado*, *Simarouba versicolor*, *Stryphnodendron obovatum*, *Tabebuia caraiba*, *Terminalia* sp., *Vitex* sp., *Vochysia tucanorum*, *Ziziphus joazeiro*, *Z. oblongifolius*.

Grassland (floodplain, herbaceous campo vegetation)

Arachis glabrata, *Ipomoea fistulosa*, *Oryza subulata*, *Panicum maximum*, *Paratheria prostrata*, *Portulaca* sp., *Setaria geniculata*, *Solanum malacoxylon*; after burning, overgrazing: *Byrsonima intermedia*, *Erythroxylum* sp.; open, grazed flooded meadows: *Bauhinia bauhinioides*, *Helicteres* sp., *Ipomoea fistulosa*, *Melochia simplex*, *Senna aculeata*, *S. alata*, *S. mucronifera*.

Freshwater Herbaceous Bog/Marsh/Swamp

Cyperus giganteus, *Paspalum repens*, *Polygonum hispidum*, *Scirpus validus*, *Thalia geniculata*, *Typha dominguensis*.

Aquatics

Ferns: *Azolla filicoides*, *Ceratopteris pteridoides*, *Marsilea polycarpa*, *Salvinia auriculata*. Angiosperms: *Aeschynomene fluminensis*, *Cabomba australis*, *C. piauhyensis*, *Echinodorus paniculatus*, *E. tenellus*, *E. uruguayensis*, *Eichhornia azurea*, *E. crassipes*, *Elodea ernstae*, *Habenaria aricaensis*, *Heteranthera limosa*, *Hydrocleys modesta*, *H. nymphoides*, *Hydrolea spinosa*, *Justicia laevilinguis*, *Lemna* sp., *Limnobium stoloniferum*, *Limnocharis flava*, *Ludwigia natans*, *L. nervosa*, *L. peruviana*, *L. sedoides*, *L. torulosa*, *Nymphaea amazonum*, *Nymphoides humboldtiana*, *N. indica*, *Paspalum repens*, *Phyllanthus fluitans*, *Pistia stratiotes*, *Pontederia corda*, *P. lanceolata*, *Reussia rotundifolia*, *R. subovata*, *Utricularia foliosa*, *U. poconensis*, *Victoria amazonica*, *V. cruziana*; on floating mats (camalotes): *Commelina* cf. *nudiflora*, *Cyperus haspan*, *Eleocharis* sp., *Oyedaea* sp., *Rhynchospora corymbosa*, *Scirpus cubensis*, *Sesbania exasperata*, *Solanum* sp.

Lower to Upper Montane Broad-Leaved Forest (moist gallery-swamp margin forest association; semi-deciduous forest association with affinities to chaco and Amazonian transition vegetation)

Gallery-swamp margin association: *Abuta grandifolia*, *Aeschynomene fluminensis*, *A. sensitiva*, *Cassia grandis*, *Cissus hassleriana*, *Coccoloba* sp., *Combretum laxum*, *Couepia uiti* (sandy places along river banks), *Croton glandulosus*, *Cupania castaneifolia*, *Eugenia* sp., *Ficus* sp., *Guarea macrophylla*, *Inga* sp., *Licania octandra*, *L. parvifolia*, *Mabea fistulifera*, *Mascagnia benthamiana*, *M. sepium*, *Mouriri guianensis*, *Paullinia pinnata*, *Pithecellobium multiflorum*, *Pterocarpus rohri*, *Rheedia brasiliensis*, *R. gardneriana*, *Rudgea cornifolia*, *Senna pendula* (also on floating islands), *Sphinctanthus microphyllus*, *Spondias lutea*, *Stigmaphyllon* sp., *Triplaris formicosa*, *T. schomburgkiana*, *Vochysia* sp., *Xylosma benthamii*.

Semi-deciduous forest association: *Acacia farnesiana*, *A. paniculata*, *Acosmium cardenasii*, *Albizzia hassleri*, *Anadenanthera peregrina*, *Aspidosperma polyneuron*, *A. pyrifolium*, *A.* cf. *ulei*, *Astronium fraxinifolium*, *Buchenavia tomentosa*, *Bumelia obtusifolia*, *Caesalpinia floribunda*, *Caryocar brasiliense* (briefly deciduous), *Coccoloba cujabensis*, *Combretum leprosum*, *Copaifera chodatiana*, *C. cordifolia*, *Dalbergia* sp., *Enterolobium contortisiliquum*, *Hymenaea courbaril*, *Machaerium acutifolium*, *Ocotea suaveolens*, *Phyllostylon rhamnoides*, *Pithecellobium saman*, *Rollinia* sp., *Salacia elliptica*, *Seguieria* sp., *Sterculia striata*, *Swartzia jorori*, *Tabebuia impetiginosa*, *T. ochracea*, *Talisia esculenta*.

APPENDIX 1.27

Selected list of lowland Neotropical rain forest species from the San Carlos de Río Negro region of southwestern Venezuela–northeastern Brazil (Clark & Liesner, 1989, in Jordon, 1989), Manaus (Prance, 1990), and Peru (Gentry & Terborgh, 1990).

Gymnosperm: *Gnetum schwackeanum*. Angiosperms: *Acacallis fimbriata*, *Acioa schultesii*, *Aciotis viscosa*, *Aechmea brevicollis*, *Aegiphila integrifolia*, *Aeschynomene evenia*, *Aldina kunhardtiana*, *Amasonia arborea*, *Amphirrox latifolia*, *Anacardium occidentale*, *Anaxagorea brachycarpa*, *Andropogon bicornis*, *Annona* cf. *gigantophylla*, *Anthurium atropurpureum*, *Apeiba* sp., *Apodandra loretensis*, *Apteria aphylla*, *Araeococcus flagellifolius*, *Aristolochia acutifolia*, *Arrabidaea egensis*, *Aspidosperma verruculosum*, *Asplundia venezuelensis*, *Axonopus capillaris*, *Bactris balanophora*, *Bellucia circumscissa*, *Bifrenaria longicornis*, *Bonafousia* sp., *Borreria latifolia*, *Brosimum utile*, *Buchenavia suaveolens*, *Byrsonima wurdackii*, *Byttneria piresii*, *Calathea acuminata*, *Callichlamys latifolia*, *Calycophyllum obovatum*, *Calyptrocarya bicolor*, *Campylocentrum huebneri*, *Campylosiphon purpurascens*, *Capsicum* sp., *Caraipa longipedicellata*, *Carpotroche grandiflora*, *Caryocar glabrum*, *Casearia arborea*, *Catostemma* sp., *Cayaponia coriacea*, *Cecropia sciadophylla*, *Cedrelinga cateniformis*, *Chaetocarpus* sp., *Chamaecrista adiantifolia*, *Cissampelos andromorpha*, *Cissus sicyoides*, *Citrullus lanatus*, *Clathrotropis* cf. *brachypetala*, *Clidemia alternifolia*, *Clitoria javitensis*, *Clusia viscida*, *Coccoloba parimensis*, *Codonanthe* sp., *Codonanthopsis ulei*, *Compsoneura debilis*, *Conceveiba guianensis*, *Connarus* sp., *Cordia naidophila*, *Couepia bernardii*, *Couma catingae*, *Coussarea brevicaulis*, *Croton trinitatis*, *Curtia* sp., *Cybianthus densiflorus*, *Cyclanthus bipartitus*, *Cyperus diffusus*, *Dialium*? sp., *Dichapetalum odoratum*, *Dictyostega orobanchoides*, *Didymopanax spruceanus*, *Dimorphandra pennigera*, *Dioclea elliptica*, *Dioscorea* sp., *Diplacrum capitatum*, *Diplasia karatifolia*, *Discophora* sp., *Distictella magnoliifolia*, *Distictis pulverulenta*, *Doliocarpus savannarum*, *Duguetia cauliflora*, *Emmotum holosericeum*, *Eperua leucantha*, *Epidendrum*

sp., *Erechtites hieraciifolius*, *Erythroxylum hypoleucum*, *Eschweilera bracteosa*, *Eupatorium cerasifolium*, *Euphronia hirtelloides*, *Euterpe* sp., *Faramea capillipes*, *Ferdinandusa goudotiana*, *Ficus guianensis*, *Gavarretia terminalis*, *Geonoma* cf. *maxima*, *Geophila orbicularis*, *Glycoxylon inophyllum*, *Goupia glabra*, *Graffenrieda candelabrum*, *Guapira cuspidata*, *Guarea cinnamomea*?, *Guatteria schomburgkiana*, *Gurania bignoniacea*, *Gustavia acuminata*, *Gymnosiphon divaricatus*, *Havetiopsis* sp., *Heliconia acuminata*, *Helicostylis scabra*, *Helmontia* sp., *Heteropsis flexuosa*, *Heterostemon* aff. *cauliflorus*, *Hevea brasiliensis*, *Hirtella schultesii*, *Homolepis aturensis*, *Humboldtiella* sp., *Humiria balsamifera*, *Hypolytrum strictum*, *Ilex laureola*, *Inga macrophylla*, *Iriartella setigera*, *Ischnosiphon polyphyllus*, *Jacaranda copaia*, *Jessenia bataua*, *Jubelina bracteosa*, *Justicia pectoralis*, *Kyllinga pumila*, *Leandra aristigera*, *Leopoldinia piassaba*, *Licania gracilipes*, *Lindernia diffusa*, *Lisianthius* cf. *chelonoides*, *Loreya minor*, *Mabea* sp., *Macrolobium canaliculatum*, *Maieta guianensis*, *Mandevilla* sp., *Manilkara* sp., *Marcgravia* sp., *Maripa paniculata*, *Markea* sp., *Martinella obovata*, *Matayba* cf. *arborescens*, *Mauritia carana*, *Maxillaria discolor*, *Maytenus* sp., *Melampodium camphoratum*, *Mendoncia cardonae*, *Mezilaurus sprucei*, *Miconia guianensis*, *Micrandra siphonioides*, *Mikania sprucei*, *Minquartia guianensis*, *Monotagma caprinense*, *Monstera adansonii*, *Mouriri uncitheca*, *Myrcia barrensis*, *Myrmidone lanceolata*, *Myrsine* sp., *Nautilocalyx* sp., *Neea obovata*, *Neocouma ternstroemiacea*, *Neoregelia eleutheropetala*, *Ocotea costulata*, *Octomeria complanata*, *Odontadenia* sp., *Oenocarpus bacaba*, *Opisthocentra clidemioides*, *Ouratea* sp., *Paepalanthus fasciculatus*, *Pagaea* sp., *Pagamea hirsuta*, *Palicourea corymbifera*, *Palmorchis* sp., *Panicum granuliferum*, *Pariana trichosticha*, *Paspalum decumbens*, *Passiflora auriculata*, *Paullinia capreolata*, *Peperomia macrostachya*, *Pera schomburgkiana*, *Perama plantaginea*, *Philodendron fragrantissimum*, *Phorodendron* sp., *Phthirusa* aff. *maculata*, *Phyllanthus orbiculatus*, *Phytolacca rivinoides*, *Picramnia platystachya*, *Piper holtii*, *Pitcairnia rubiginosa*, *Pithecellobium laetum*, *Pleonotoma dendrotricha*, *Pleurothallis* sp., *Plukenetia brachybotrya*, *Polycycnis vittata*, *Poraqueiba sericea*, *Portulaca rubricaulis*, *Potalia amara*, *Pourouma tomentosa*, *Protium* sp., *Psittacanthus* sp., *Psychotria adderleyi*, *Qualea esmeraldae*, *Quiina pteridophylla*, *Rapatea longipes*, *Retiniphyllum concolor*, *Rhodognaphalopsis humilis*, *Rhynchospora pubera*, *Rinorea macrocarpa*, *Roucheria* aff. *punctata*, *Rudgea ayangannensis*, *Sabicea oblongifolia*, *Sacoglottis mattogrossensis*, *Sauvagesia erecta*, *Schiekia orinocensis*, *Schistostemon* cf. *retusum*, *Schlegelia violacea*, *Schwenckia americana*, *Sciadotenia sprucei*, *Sciaphila albescens*, *Securidaca* cf. *retusa*, *Senna bacillaris*, *Sipanea pratensis*, *Siparuna* cf. *guianensis*, *Sloanea maroana*, *Solanum altissimum*, *Sorocea muriculata*, *Sparattanthelium* sp., *Stenospermation* cf. *steyermarkii*, *Sterigmapetalum guianense*, *Strychnos guianensis*, *Swartzia cupavenensis*, *Symphonia globulifera*, *Tabernaemontana* sp., *Tapirira guianensis*, *Ternstroemia* sp., *Tetragastris* cf. *panamensis*, *Tetrameranthus duckei*, *Tetrapterys mucronata*, *Tococa guianensis*, *Trichilia schomburgkii*, *Unonopsis stipitata*, *Urospatha sagittifolia*, *Vantanea* sp., *Vitex klugii*, *Vochysia complicata*, *Vriesea socialis*, *Wullschlaegelia aphylla*, *Xyris esmeraldae*, *Zornia latifolia*.

Additional genera represented at the Reserva Florestal Adolpho Ducke (Manaus, Amazonas, Brazil; Prance, 1990): *Corythophora rimosa*, *Couepia bracteosa*, *Couratari multiflora*, *Lecythis pisonis*, *Parinari campestris*, *Pseudoconnarus macrophyllus*, *Rhabdodendron amazonicum*, *Tapura amazonica*.

Additional genera represented in the Cocha Cashu floodplain forest (Manu National Park, Peru; Gentry & Terborgh, 1990): *Ampelocera* sp., *Astrocaryum murumuru*, *Batocarpus costaricensis*, *Caryodaphnopsis fosteri*, *Clarisia racemosa*, *Cremastosperma leiophyllum*, *Diospyros artanthifolia*, *Huertea glandulosa*, *Iriartea deltoidea*, *Iryanthera olacoides*, *Leonia glycycarpa*, *Lonchocarpus spiciflorus*, *Lunania parviflora*, *Otoba parvifolia*, *Oxandra espintana*, *Poulsenia armata*, *Pouteria ephedrantha*, *Pseudolmedia laevis*, *Quararibea wittii*, *Ruizodendron ovale*, *Scheelea* sp.

APPENDIX 2

Late Cretaceous and Cenozoic plants mentioned in the text

2.1 (Arranged by age; families fide original authors)
2.2 (Arranged by plant group/family; families fide original authors)

The primary data for the listings are in Tables 4.1 (Mexico), 5.1 (the Antilles), 6.1 (Central America), 7.1 (South America, Cretaceous and Paleogene), 7.2 (South America, Neogene), and 7.6 (South America, Quaternary). The following key is provided to facilitate reference between the tables and appendices:

Table 4.1 Mexico
- Refs. 1–8 Cretaceous
- Refs. 9–11 Eocene
- Refs. 12–21 Oligocene, Oligo–Miocene
- Refs. 22–25 Miocene
- Ref. 26 Pliocene
- Refs. 27–39/40 Quaternary
- Refs. 41, 42 Undifferentiated

Table 5.1 The Antilles
- Refs. 1–3 Cretaceous
- Refs. 4–7 Eocene
- Refs. 8–10 Oligocene
- Refs. 11–20 Miocene
- Refs. 21–24 Quaternary

Table 6.1 Central America
- Ref. 1 Cretaceous
- Ref. 2 Eocene
- Refs. 3, 4, 6–11 Miocene, Mio–Pliocene
- Refs. 5, 12–15 Pliocene, Plio–Pleistocene
- Refs. Q1–Q23 Quaternary

Table 7.1 South America, Cretaceous–Paleogene (Paleocene, Eocene, Oligocene)

Refs. 1–52 Argentina
- 1–20 Cretaceous (Ref. 15 is mostly Eocene)
- 21–37 Paleocene
- 38–47 Eocene (47 now Miocene; Zamola, 2000, ref. see Chapter 7)
- 48–52 Oligocene

Refs. 53–64 Chile
- 53–55 Cretaceous
- 56 Paleocene
- 57–61 Eocene
- 62–64 Oligocene

Refs. 65–66 Bolivia
- 65 Late Cretaceous–Paleocene
- 66 Late Eocene–early Oligocene

Refs. 67–71 Peru
- 67, 68 Cretaceous
- 69–71 Eocene

Ref. 72 Ecuador, Eocene

Refs. 73–87 Colombia
- 73, 74, 78d–82 Cretaceous
- 83–85 Paleocene
- 75–78a, 86, 87 Eocene
- 78b, c Oligo–Miocene

Refs. 88–92 Venezuela
- 90 Cretaceous
- 88, 89, 91, 92 Eocene

Refs. 93–96 Guianas
- 93 Cretaceous
- 94 Cretaceous (pollen zones A–B1)
  - Paleocene (pollen zone B2)
  - Eocene (pollen zones C, D)
  - Oligocene to early Miocene (pollen zones E, F)
  - Quaternary (pollen zone G)
- 95, 96 Paleocene

Refs. 97–100 Brazil
- 97a, 99, 100 Cretaceous
- 97b Paleocene
- 98 Eocene

Table 7.2 South America, Neogene (Miocene, Pliocene)

Refs. 1–13 Argentina
- 1–6, 8–13 Miocene
- 7 Pliocene

Refs. 14–19b Chile, Miocene

Refs. 20–27 Bolivia
- 20–22 Miocene
- 23–27 Pliocene

Refs. 28a, b Peru, Miocene

Refs. 29–31 Ecuador, Miocene

Refs. 32–39 Colombia
- 32–35, 37 Miocene
- 36, 38, 39 Pliocene

Refs. 40–43 Venezuela, Miocene

Refs. 44, 45 Trinidad, Miocene

Refs. 46–50 Brazil
- 50 Miocene
- 46–49 Pliocene

Table 7.6 South America, Quaternary
- Refs. 1–7 Argentina, Tierra del Fuego
- Refs. 8–12 Chile
- Ref. 13 Bolivia
- Refs. 14, 15 Peru
- Refs. 16, 17 Ecuador
- Refs. 18, 19 Galápagos Islands
- Ref. 20 Colombia
- Refs. 21–25 Venezuela
- Ref. 26 Trinidad
- Refs. 27–33 Brazil

APPENDIX 2.1

Late Cretaceous and Cenozoic plants mentioned in the text, arranged by age. Numbers in parentheses refer to the tables in the text (4.1 = Mexico; 5.1 = Antilles; 6.1 = Central America [Quaternary references are listed separately and designated with a (Q)]; 7.1 = South America, Late Cretaceous and Paleogene; 7.2 = South America, Neogene; 7.6 = South America, Quaternary) and to references cited in the legends of the tables (e.g., 4.1-1), where extended information on the age, formation, location, taxonomic group, and literature for each taxon may be found. For bibliographic references cited in the Appendix see References in Chapters 4–7. Multiple listings for a single taxon may include some aff., cf., type, and ? identifications. In some instances where only a single taxon is described from a site, that taxon is listed in the Appendix (with bibliographic reference) but not in the table.

Cretaceous

(Including some Late Jurassic/Early Cretaceous and Late Cretaceous–Paleogene transition floras; 7.1-8 includes some transition elements into the early Eocene)

Fungi

Brefeldiellites argentina (7.1-4), *Callimothallus corralescence* (7.1-79), *Fusiformisporites lineolatus* (7.1-80), *F. polyhedricus* (7.1-100), *Microthyriacites baqueroensis* (7.1-4), *Molinea asterinoides* (7.1-79), *Monoporisporites grandis* (7.1-80), *Trichopeltinites pulcher* (7.1-4).

Algae and allied groups

Botryococcus (7.1-20), *B. braunii* (7.1-65), *Pediastrum* (7.1-20), *P. paleogeneites* (7.1-100), *Pterospermella* (7.1-74), *Schizocystia* (7.1-74). Acritarchs: *Diplotesta inflata* (5.1-3), *Palaeostomocystis fragilis* (5.1-3), *Prismatocystis ewingii* (5.1-3). Hystrichosphaerids: *Hystrichosphaeridium* (5.1-3), *H. arundum* (5.1-3), *Subtilisphaera* (7.1-74). Dinoflagellates: *Canningia minor* (5.1-3), *Cometodinium whitei* (7.1-74), *Scriniodinium* (5.1-3), *Stephodinium* cf. *europaicum* (5.1-3). Plankton: *Confossia vulgaris* (7.1-11), *C. rara* (7.1-11), *Patera crassa* (7.1-11), *P. tenuis* (7.1-11), *Schizosporis reticulatus* (7.1-10).

Bryophyta (some may be considered fern spores by some authors)

Aequitriradites baculatus (7.1-74), *Coptospora* (7.2-2), *C. foveolata* (7.1-2, 5), *Foraminisporis asymmetricus* (7.1-5), *F. dailyi* (7.1-5), *Naiaditaspora gemmata* (7.1-5), *Staplinisporites caminus* (7.1-5), *Stoverisporites lunaris* (7.1-5), *Taurocusporites segmentatus* (7.1-10), *Triporoletes reticulatus* (7.1-10).

Ferns and allied groups

Achradosporis lurensis (7.1-19), *Adiantum patagonicum* (7.1-8), *Aequitriradites* (7.1-10, 100), *A. baculatus* (7.1-5, 74), *A. spinulosus* (7.1-2, 3, 5), *A. verrucosus* (7.1-2, 3, 5), *Antulsporites baculatus* (7.1-3), *Apiculatisporis* (7.1-74), *Appendicisporites* (7.1-80), *A.* cf. *stylosus* (7.1-3), *Aratrisporites ocellatus* (7.1-99), *Ariadnaesporites micromedusus* (7.1-11), *A. spinosus* (7.1-100), *Asterisporites chlonovae* (7.1-3), *Auriculozonospora spongiosa* (7.1-4), *Auritulinasporites* (7.1-5, 74), *Azolla* (7.1-17, 19, 20, 65), *A. polyancyra* (7.1-11), *Baculatisporites comaumensis* (7.1-2, 5, 74), *B. multibaculae* (7.1-80, 81), *Bacutriletes guttula* (7.1-4), *B. triangulatus* (7.1-4), *Baqueroites padulae* (7.1-4), *Biretisporites* (7.1-2, 5, 19), *B. potoniaei* (7.1-74, 90, 99), *Blechnum* (7.1-9), *Buttinia andreevi* (7.1-80, 81), *Cadiospora* (7.1-74), *Calamospora* (5.1-3), *C. mesozoica* (7.1-5, 65), *Callialasporites dampieri* (7.1-90), *Camarazonosporites* (7.1-74, 99), *C. microalveolatus* (7.1-5), *Carbochonicus carbunculus* (7.1-4), *Caudaspora spinosa* (7.1-67, 68), *C. verrucata* (7.1-67, 68), *Ceratosporites* (7.1-10, 99), *C. equalis* (7.1-5), *C. setosus* (7.1-5), *Chomotriletes minor* (7.1-5, 74), *Cibotiidites* (7.1-74, 80), *C. auriculatus* (7.1-5), *Cicatricosisporites* (5.1-3; 7.1-10, 11), *C. annulatus* (7.1-5, 74), *C. australiensis* (7.1-2, 3, 5, 10, 74, 90), *C. avnimelechi* (7.1-90), *C. baculatus* (7.1-100), *C. baqueroensis* (7.1-5), *C. berouensis* (7.1-74), *C. brevilaesuratus* (7.1-99), *C. crassiterminatus* (5.1-2), *C. cristatus* (7.1-100), *C. dorogensis* (7.1-90, 100), *C.* cf. *ethmos* (7.1-5), *C. giganteus* (7.1-5), *C. hallei* (7.1-74, 99), *C. hughesii* (7.1-3, 5, 10), *C. mediostriatus* (7.1-99), *C. microstriatus* (7.1-99), *C. nuni* (7.1-99), *C. patomacensis* (7.1-90), *C. recticiatricosus* (7.1-90), *C. subrotundus* (7.1-74, 90, 99), *C. ticoensis* (7.1-5), *C. venustus* (7.1-78d, 99, 100), *Cingulatisporites verrucatus* (7.1-90, 100), *Cladophlebis antarctica* (7.1-4), *C. browniana* (7.1-4), *C. haiburnensis* var. *rectimarginata* (7.1-4), *C. patagonica* (7.1-4), *C. tripinnata* (7.1-4), *Clavatriletes disparilis* (7.1-100), *Clavifera* (7.1-5), *C. triplex* (7.1-17), *Conbaculatisporites* (7.1-17), *Concavisporites* (7.1-90), *C. jurienensis* (7.1-74), *C. lamontis* (5.1-3), *C.* cf. *laticrassus* (7.1-5), *Concavissimisporites* (7.1-3), *C. minor* (7.1-74), *C. punctatus* (5.1-2; 7.1-74), *Contignisporites cooksonii* (7.1-2, 3, 5, 10), *C. fornicatus* (7.1-3, 90), *Converrucosisporites* (7.1-2, 17), *C. proxigranulatus* (7.1-93), *C. saskatchewanensis* (7.1-74), *Coptospora* (7.1-2, 90), *C. foveolata* (7.1-5), *Couperisporites complexus* (7.1-3), *Crybelosporites* (7.1-10), *C.* cf. *brenneri* (7.1-99), *Cyathea cyathifolia* (7.1-4), *Cyatheacidites tectifera* (7.1-3, 5), *C. vanderhammeni* (7.1-80, 81), *Cyathidites* (7.1-65), *C. australis* (5.1-3; 7.1-2, 5, 55, 90, 93, 99), *C. minor* (5.1-3; 7.1-5, 55, 74, 90, 93, 99), *C./Deltoidospora* (7.1-78d), *Cyclogranisporites* (7.1-74), *Deltoidospora* (7.1-2, 80), *D. australis* (7.1-19, 20), *D. hallii* (7.1-74, 99), *D. juncta* (7.1-74), *D. minor* (5.1-2; 7.1-5, 17, 19, 20), *D. nana* (7.1-93), *D. neddeni* (7.1-19), *D. quiriquinaensis* (7.1-55), *D. tenuis* (7.1-99), *Dennstaedtia patagonica* (7.1-8, 14), *Densoisporites* (7.1-99), *D. corrugatus* (7.1-3, 5), *D. microrugulatus* (7.1-93), *D. velatus* (7.1-2, 3, 5), *Dicksoniopsis coniopteroides* (6.1-1), *Dictyophyllidites* (5.1-2; 7.1-2), *D. harrisii* (7.1-74), *D. equiexinus* (7.1-90), *D. mortoni* (7.1-17, 19), *Discisporites discoides* (5.1-3), *Distaltriangulisporites* cf. *perplexus* (7.1-74), *Divisisporites* cf. *maximus* (7.1-74), *Dorfiella auriculata* (4.1-2), *Dryopterites problematicus* (7.1-8, 14), *Duplexisporites* (7.1-2, 3), *Duplosporis* (7.1-55), *Echinatisporis varispinosus* (7.1-74), *Echitriletes muelleri* (7.1-100), *Elaterocolpites castelaini* (7.1-74, 78d), *Elateroplicites africaensis* (7.1-78d), *Elaterosporites klaszi* (7.1-74, 78d), *E. verrucatus* (7.1-74), *Equisetites* (7.1-4, 97a), *Erlansonisporites sparsis* (7.1-4), *Favososporites* (*Horstisporites*) *feruglioi* (7.1-7), *F.*

spinulosus (7.1-7), *Foraminisporis asymmetricus* (7.1-5), *F. dailyi* (7.1-3, 5, 10), *F. microgranulatus* (7.1-3), *F. variornatus* (7.1-3), *F. wonthaggiensis* (7.1-3, 10, 74), *Foveotriletes* (7.1-90), *F. margaritae* (7.1-94), *Gabonisporis vigourouxii* (7.1-65, 100), *Gemmatriletes clavatus* (7.1-65, 74, 99), *G.* cf. *densegemmatus* (7.1-74), *Gleichenia* (7.1-9), *Gleicheniidites* (microfossils) (5.1-3; 7.1-11, 20), *G. apilobatus* (5.1-3; 7.1-90), *G. argentinus* (7.1-56), *G.* aff. *cercinidites* (7.1-2)/*G. circinidites* (5.1-3), *G. marciae* (5.1-3), *G. senonicus* (5.1-2, 3; 7.1-5, 10, 17, 19), *G. severus* (5.1-3), *Gleichenites* (megafossils) (5.1-1), *G. argentinica* (7.1-4), *G. feruglioi* (7.1-4), *G. piatnitzkyi* (7.1-8, 14), *G. san-martinii* (7.1-4), *G. vegagrandis* (7.1-4), *Granulatisporites* (7.1-17), *Grapnelispora* (7.1-20), *G. evansii* (7.1-18), *Hamulatisporis* (7.1-17, 74), *H. hamulatis* (7.1-90), *Hausmannia papilio* (7.1-4), *H. patagonica* (7.1-4), *Heliosporites baculatus* (7.1-5; *Antulsporites baculatus*), *Henrisporites elegans* (7.1-6), *H. heteracanthus* (7.1-7), *H. musacchioi* (cf. *Isoetes*; 7.1-6), *Horriditriletes* (7.1-2), *Horstisporites feruglioi* (7.1-4), *H. iridodea* (7.1-4), *Hughesisporites patagonicus* (7.1-4), *H. rugulatus* (7.1-4), *Hymenophyllum* (7.1-9), *H. priscum* (7.1-8, 53), *Hypocrititriletes insolitus* (7.1-9), *Impardecispora* (7.1-78d), *I. trioreticulosa* (7.1-74), *Interulobites distannulatus* (7.1-3), *I. intraverrucatus* (7.1-3, 10), *I. pseudoreticulatus* (7.1-3), *I. triangularis* (7.1-2, 10), *I. variabilis* (7.1-19), *Ischyosporites* (7.1-17), *Isoetites* (7.1-97a), *Klukisporites* (7.1-74), *K. elongatus* (7.1-93), *K. labiatus* (7.1-2), *K. pachydictyus* (7.1-17), *K. scaberis* (7.1-3, 99), *K. tuberosus* (7.1-3), *K. variegatus* (7.1-90, 100), *Kraeuselisporis* (7.1-74), *Laevigatosporites* (5.1-3; 7.1-74), *L. belfordii* (7.1-3, 5), *L. dehiscens* (7.1-55), *L.* cf. *discordatus* (7.1-17), *L. gracilis* (7.1-17, 93), *L. ovatus* (5.1-3; 7.1-5, 16, 17, 20), *L. vulgaris* (7.1-17), *Leiotriletes* (7.1-16, 55), *L. giganteus* (7.1-80), *L. guaduensis* (7.1-81, 82), *L. regularis* (7.1-5), *Leptolepidites* (7.1-17, 78d), *L. macroverrucosus* (7.1-3), *L. major* (7.1-5, 90), *L. proxigranulatus* (7.1-3, 10), *L. psarosus* (7.1-99), *L. verrucatus* (7.1-90), *Lycopodiumsporites* (7.1-17, 78d, 80), *L. austroclavatidites* (7.1-2), *L. clavatoides* (5.1-3), *L. facetus* (7.1-99), *L. novomexicanum* (7.1-100), *L. paleocenicus* (7.1-90), *Lygodioisporites* (7.1-80), *Lygodiumsporites* (7.1-2), *Magnastriatites howardii* (7.1-100), *Marattisporites scabratus* (7.1-17), *Matonisporites* (7.1-10, 99, 100), *M.* cf. *dorogenis* (7.1-93), *M. equiexinus* (7.1-93), *M. guianensis* (7.1-93), *M. tenuilabratus* (7.1-2, 3), *Mesosingeria mucronata* (7.1-4), *M.* (?) *obtusa* (7.1-4), *M. striata* (7.1-4), *Microfoveolatosporis* (5.1-2; 7.1-5, 74), *Minerisporites* (7.1-74), *M. cheblii* (7.1-6; *Isoetes*), *M. elegans* (7.1-4), *M. holobrochatus* (7.1-7), *M. laceratus* (7.1-4), *M. patagonicus* (7.1-4), *Monosulcites* (7.1-90), *Muerrigerisporis americanus* (7.1-80), *M.* (?) *sanadriensis* (5.1-2), *Muricingulisporis* (7.1-2), *M. annulatus* (7.1-3, 5), *Naiaditaspora gemmata* (7.1-5), *Neoraistrickia* (7.1-5, 17, 74), *Nodosisporites* (7.1-10), *Obtusisporis obtusangulus* (7.1-5), *Ornamentifera tuberculata* (7.1-5), *Osmundacidites diazii* (7.1-5), *O. wellmanii* (7.1-2, 74), *Peromonilites fragilis* (7.1-93), *Perotriletes pannuceus* (7.1-78d, 90, 99, 100), *Phlebopteris* (7.1-74), *Pilosisporites trichopapillosus* (7.1-93), *Polycingulatisporites trabeculatus* (7.1-3), *Polypodiaceoisporites elegans* (7.1-5), *P. potoniei* (7.1-100), *Polypodiidites* (7.1-2, 5, 17), *P. inangahuensis* (7.1-55), *Psilatriletes circumundulatus* (7.1-93), *Punctatisporites scabratus* (7.1-74), *Punctato[i]sporites* (7.1-55), *P. major* (7.1-74), *Pustulatisporites* (7.1-20), *Quiriquinaspora chilensis* (7.1-55), *Retimonocolpites* (7.1-90), *Reticulatisporites* (7.1-2, 80), *R. jardinus* (7.1-99), *R. ornatus* (7.1-5), *Retitriletes* (7.1-74), *R. austroclavatidites* (7.1-5, 19), *R. baqueroense* (7.1-5), *Rotverrucosisporites* (7.1-2, 3), *R. labratus* (7.1-5), *Rotverrusporites rupununiensis* (7.1-93), *Rouseisporites reticulatus* (7.1-5), *Ruffordia goepperti* (7.1-4), *Rugulatisporites neuquenensis* (7.1-5), *Salvinia coahuiensis* (4.1-3), Schizaeaceae (7.1-97a), *Schizaeoisporites* (7.1-3), *S. cicatricos* (7.1-80), *S. rectangularis* (7.1-80), *Schizea certa* (7.1-90, 100), *S. reticulata* (7.1-90), *Schizosporis* (7.1-80), *Sergipea* (7.1-74), *S. naviformis* (7.1-90, 99), *S. variverrucata* (7.1-99), *Sestrosporites* (7.1-2), *S. pseudoalveolatus* (7.1-5, 74), *Sphenopteris* cf. *fittonii* (7.1-4), *S. goepperti* (7.1-4), *S. patagonica* (7.1-4), *S.* (*Onychiopsis*) *psilotoides* (7.1-4), *Staplinisporites caminus* (7.1-2, 3, 5), *Stereisporites antiquasporites* (7.1-17), *S. pilatus* (7.1-99), *S. stereoides* (5.1-2), *Stoverisporites lunaris* (7.1-5), *Taurocusporites reduncus* (5.1-3), *T. segmentatus* (7.1-3, 5, 10), *Thecaspora spinosa* (7.1-67, 68), *Thyrsopteris antiqua* (7.1-8, 53), *Todisporites major* (7.1-17, 19, 99), *T. minor* (5.1-3; 7.1-19), *Triletes* (7.1-99, 100), *T.* cf. *parvallatus* (7.1-55), *T.* cf. *tuberculiformis* (7.1-2), *Trilobosporites* (7.1-2), *T. apiverrucatus* (7.1-3, 5), *T. canadensis* (7.1-3), *T. purverulentus* (7.1-3, 5), *T. trioreticulosus* (7.1-5, 10), *Triporoletes reticulatus* (7.1-3, 10), *Tuberculatosporites* (7.1-5, 99), *Undulatisporites takutuensis* (7.1-93), *U. undulapolis* (7.1-93), *Uvaesporites* (7.1-74, 78d), *Vallizonosporites spinosus* (7.1-5), *Velosporites* (7.1-90), *Verrucosisporites* (7.1-3, 5, 10, 90), *V. rotundus* (7.1-74), *Verrutriletes tomtaylori* (7.1-4), *Vitreisporites pallidus* (7.1-93), *Waltzispora* (7.1-17), *Weichselia reticulata* (7.1-74), *Zlivisporis* (7.1-67, 68), *Z. blanensis* (7.1-100), *Zonalapollenites* [?, spore] (7.1-90).

Gymnosperms

(For note on listings under 7.1-99 below, see Table 7.1, Ref. 99)

Aachenia knoblochi (4.1-4), cf. *Abietineaepollenites* (7.1-93), *Acmopyle antarctica* (7.1-8, 53), ?*Alaticolpites limai* (7.1-99), *Alisporites* (7.1-2, 10), *A. australis* (7.1-20), *A. bilateralis* (5.1-3), *Alkastrobus peltatus* (7.1-Chapter 7, Del Fuego & Archangelsky, 2005), *Allicospermum patagonicum* (7.1-4), *Almargemia incrassata* (7.1-4), *Applanopsis dampieri* (7.1-74), *A. segmentatus* (7.1-74), *A. trilobatus* (7.1-74), *A. turbatus* (7.1-74), *Apterocladus lanceolatus* (7.1-4, 5), *Araucaria* (4.1-1), *A. grandifolia* (7.1-4), *Araucariacites* (7.1-5, 12, 81), *A. australis* (5.1-2; 7.1-2, 20, 65, 74, 78d, 93, 100), *A. guianensis* (7.1-74, 93, 99), *A. limbatus* (5.1-3; 7.1-99), *Araucariostrobus* (7.1-97a), *Araucarioxylon doeringii* (7.1-54), *A. kellerense* (7.1-54), *A. ohzuanum* (7.1-54), *A. parachoshiense* (7.1-54), *A. pichasquense* (7.1-54), *A. pseudoparenchymatosum* (7.1-54), *A. quiriquineanum* (7.1-54), *Araucarites* (6.1-1), *A. baqueroensis* (7.1-4), *A. minimus* (7.1-4), *Athrotaxis ungeri* (7.1-4), *Balmeiopsis* (7.1-5), *B. limbatus* (7.1-3, 74), Bennettitales (7.1-97a), *Bennettitaepollenites minimus* (7.1-99), *Brachyphyllum* (4.1-1, 5; 5.1-1, 5; 7.1-5, 74, 97a), *B. brettii* (7.1-4), *B. irregulare* (7.1-4, 5), *B. mamillare* (7.1-1), *B. mirandai* (7.1-4), *B. mucronatum* (7.1-4), *B. tigrense* (7.1-4; with *Podocarpidites*-type pollen), *Brunoa santarosensis* (7.1-Chapter 7, Artabe et al., 2004), *Callialasporites* (7.1-5), *C. dampieri* (7.1-10, 78d), *C. trilobatus* (7.1-2, 19, 20), *Cerebropollenites macroverrucosus* (7.1-74), *C. mesozoicus* (7.1-93), *Circulina minima* (7.1-99), *C. parva* (7.1-99), *Classopollis* (7.1-2, 10, 12, 20, 65, 74, 78d), *C. classoides* (7.1-19, 100), *C. intrareticulatus* (7.1-99), *C. jardinei* (7.1-90), *C. obidosensis* (7.1-

90), *C. torosus* (7.1-90, 93, 99), Coniferales (7.1-97a), *Coptospora striata* (7.1-3), *Corollina* (7.1-10), *Cratonia cotyledon* (7.1-97a), *Cupressinocladus leptocaldoides* (7.1-74), *C. pompeckji* (7.1-74), *Cupressioxylon mochaense* (7.1-54), *C. parenchymatosum* (7.1-54), Cycadales (7.1-97a), *Cycadolepis baqueroensis* (7.1-4), *C. coriacea* (7.1-4), *C. involuta* (7.1-4), *C. lanceolata* (7.1-4), *C. menendezii* (7.1-4), *C. oblonga* (7.1-4), *C. petriellai* (7.1-4), *Cycadopites* (5.1-2), *C.* cf. *fragilis* (7.1-93), *C. granulatus* (7.1-20), *C. minimus* (7.1-74), *C. nitidus* (7.1-2, 74, 99), *Cyclusphaera* (?) (7.1-10; see also under angiosperms Incertae sedis), *C. crassa* (7.1-3), *C. patagonica* (7.1-3), *C. psilata* (7.1-3, 5), *C. radiata* (7.1-3), *Dacrydium* (7.1-9), *Dacrycarpites* cf. *australiensis* (7.1-12), *Dacrydiumites florinii* (7.1-12, 16), *Dictyozamites areolatus* (7.1-4), *D. grandis* (7.1-4), *D. latifolius* (7.1-4), *D. minusculus* (7.1-4), *Elatocladus* (7.1-4), *Ephedripites* (7.1-19, 80, 81, 93), *E. ambonoides* (7.1-90), *E. barghoornii* (7.1-65, 78d, 90), *E. jansonii* (7.1-65), *E. montanaensis* (7.1-65), *E. pentacostatus* (7.1-100), *E. procerus* (7.1-90), *E. strigatus* (7.1-65, 90), *E. subtilis* (7.1-100), *E. undulatus* (7.1-100), *E. validus* (7.1-90), *Equisetosporites ambiguus* (7.1-74), *E. concinnus* (7.1-99), *E. costaliferous* (7.1-74, 99), *E. dudarensis* (7.1-74), *E. elongatus* (7.1-99), *E. fragilis* (7.1-99), *E. irregularis* (7.1-99), *E. leptomatus* (7.1-74), *E. minuticostatus* (7.1-20, 99), *E. mollis* (7.1-74), *E.* cf. *procerus* (7.1-99), *E. strigatus* (7.1-99), *E.* cf. *subcircularis* (7.1-74, 99), *E. translucidus* (7.1-74), *Eucommiidites* (5.1-3; 7.1-90), *E. minor* (7.1-74, 78d, 93), *E. troedsonii* (5.1-2; 7.1-93), *Exesipollenites tumulus* (7.1-93, 99), *Frenelopsis* (5.1-1), *Gamerroites psilasaccus* (7.1-5, 19), *G. volkheimeri* (7.1-5), *Ginkgoites ticoensis* (7.1-4), *G. tigrensis* (7.1-4), *Gliscopollis* (7.1-2), *Gnetaceapollenites* (7.1-90), *G. boltenhagenii* (7.1-74), *G. clathratus* (7.1-100), *G. crassipoli* (7.1-100), *G. diversus* (7.1-100), *G. jansonii* (7.1-99), *G. oreadis* (7.1-99), *G. retangularis* (7.1-99), *G. similis* (7.1-100), Gnetales (7.1-97a), *Inaperturopollenites* (7.1-78d, 81, 99), *I. dubius* (5.1-3; 7.1-74), *I. giganteus* (7.1-93), *I. hiatus* (5.1-2, 3), *I. laevigatus* (7.1-55), *I. microclavatus* (7.1-100), *I.* aff. *scabratus* (5.1-2), *I. simplex* (7.1-100), *Karkenia incurva* (7.1-4), *Kobalostrobus olmosensis* (4.1-6), *Ktalenia circularis* (7.1-4), *Lindleycladus* (7.1-97a), *Mesodescolea plicata* (7.1-4), *Mesosingeria coriacea* (7.1-4), *M. herbstii* (7.1-4), *M. mucronata* (7.1-4), *M.* (?) *obtusa* (7.1-4), *M. parva* (7.1-4), *M. striata* (7.1-4), *Metapodocarpoxylon libanoticum* (7.1-74), *Microcachryidites* (7.1-20), *M. antarcticus* (7.1-2, 11, 12, 19), *Monocolpopollenites* (7.1-99), *Monosulcites* (7.1-78d), *M. chaloneri* (5.1-3; 7.1-99), *M.* cf. *granulatus* (7.1-16), *M. inspissatus* (5.1-3), *M. minimus* (5.1-3; 7.1-65), *M. pseudospinosus* (7.1-16), *Morenoa fertilis* (7.1-4), *Nilssonia clarkii* (7.1-4), *Nothopehuen brevis* (7.1-4), orbiculas (Ubisch bodies from male cones of *Apterocladus lanceolatus* and others; 7.1-5), nucellus of *Caytonia* (7.1-74), *Otozamites archangelskyi* (7.1-1), *O. ornatus* (7.1-4), *O. parviauriculata* (7.1-4), *O. waltonii* (7.1-4), *Pachypteris elegans* (7.1-4), *P.*(?) *patagonica* (7.1-4), *Parvisaccites majesticus* (5.1-3), *P. radiatus* (5.1-3; 7.1-55), *Peltandipites* (7.1-99), *Penetetrapites mollis* (7.1-99), *Phoenicopsis* cf. *speciosa* (5.1-1), *Phrixipollenites* (7.1-20), *Phyllocladidites mawsonii* (7.1-12, 55), *Phyllocaldoxylon antarcticum* (7.1-54), *P. aparenchymatosum* (7.1-54), *Piceapollenites* (7.1-55), *P. alatus* (5.1-3), *Pinuspollenites concepcionensis* (7.1-55), *Platysaccus elizabethae* (5.1-3), cf. Podocarpaceae (7.1-5), *Podocarpidites* (7.1-10, 12, 100), *P.* cf. *ellipticus* (7.1-2), *P. marwickii* (7.1-12, 16, 19), *P. microreticuloidata* (7.1-12), *P. multesimus* (7.1-55), *P. psilasaccus* (7.1-12), *P. rugulosus* (7.1-19), *P. verrucosus* (7.1-19), *P.* sp. (7.1-12), *Podocarpoxylon* (4.1-5), *P. paleoandium* (7.1-54), *P. paleosalignum* (7.1-54), *Podocarpus* (7.1-9), *P. dubius* (7.1-4), *P. inopinatus* (7.1-8, 53), *P.? palissyafolia* (7.1-4), *P. tertiaria* (7.1-8), *Podosporites microsaccatus* (7.1-11), *Podozamites* (7.1-74), *P.* cf. *eichwaldii* (5.1-1), *Protophyllocladoxylon rosablancaense* (7.1-73, 74), *Protophyllocladus australis* (7.1-8, 14), *Proxapertites* (7.1-80, 81), *Pseudoaraucaria valentini* (7.1-8, 53), *Pseudoctenis* (7.1-74), *P. crassa* (7.1-4), *P. dentata* (7.1-4), *P. ensiformis* (7.1-4), *P. giganteus* (7.1-4), *P. ornata* (7.1-4), *Pterophyllum trichomatosum* (7.1-4), *Pteruchipollenites crenulatus* (5.1-3), *P. transversus* (5.1-2), *Ptilophyllum acutifolium* (7.1-4), *P. angustus* (7.1-1), *P. hislopii* (7.1-4), *P. longipinnatum* (7.1-4), *Raritania* (4.1-6), *Ruflorinia papillosa* (7.1-4), R. *pilifera* (7.1-4), R. *sierra* (7.1-4), *Singhia minima* (7.1-99), *S. montanaensis* (7.1-99), *Spheripollenites psilatus* (5.1-3; 7.1-65), *S. subgranulatus* (7.1-74), *Squamastrobus tigrensis* (7.1-4), *Steevesipollenites alatiformis* (7.1-100), *S. amphoriformis* (7.1-100), *S. binodosus* (7.1-100), *S. cupliformis* (7.1-99), *S. duplibaculum* (7.1-100), *S. giganteus* (7.1-100), *S. grambasti* (7.1-99), *S. multilineatus* (7.1-100), *S. nativensis* (7.1-100), *Sueria elegans* (7.1-4), *S. rectinervis* (7.1-4), *Taeniopteris* (7.1-4), *Tarphyderma glabra* (7.1-4), *Taxodiaceapollenites* cf. *hiatus* (7.1-65), *Taxodioxylon* (4.1-5), *T. pseudocompressum* (7.1-54), *Ticoa harrisii* (7.1-4), *T. lamellata* (7.1-4), *T. marginipinnulata* (7.1-4), *Tomaxellia biforme* (7.1-4, with *Classopollis* pollen; 7.1-5), *T. degiustoi* (7.1-4), *Triangulopsis* (7.1-99), *Trifossapollenites* (7.1-74), *Trisaccites microsaccatus(m)*, (7.1-10, 12, 16, 55), *Trisacocladus tigrensis* (7.1-4, 5), *Tsugaepollenites mesozoicus* (7.1-55), *Vitreisporites pallidus* (5.1-3; 7.1-2), *Welwitschiella austroamericana* (7.1-97a), *Welwitschiophyllum brasiliense* (7.1-97a), *Welwitschiostrobus murili* (7.1-97a), *Williamsonia bulbiformis* (7.1-4), *W. umbonata* (7.1-4), *Worsdellia bonettiae* (7.1-Chapter 7, Artabe et al., 2004), *Yuccites* (5.1-1), *Zamites* cf. *buchianus* (5.1-1), *Z. decurrens* (7.1-4), *Z. grandis* (7.1-4), *Z.* cf. *tenuinervis* (5.1-1; 7.1-74), *Zonalapollenites dampieri* (5.1-3).

Angiosperms

Angiosperm leaves (unidentified; 7.1-4), *Acacioxylon pseudocavenium* (7.1-54), *Afropollis jardinus* (7.1-78d; see also Incertae sedis), *Ailanthipites* (7.1-19), *Alaticolpites limai* (7.1-99, 100), *Alnipollenites trina* (4.1-8), *Amomyrtoxylon paleolumum* (7.1-54), *Anacardites rioturbioensis* (?) (7.1-15; now Danian), *Anacolosidites* (7.1-16), *A. diffusa* (7.1-19), *A.* cf. *luteoides* (7.1-100), *Apoci[y]nophyllum chalianum* (7.1-8), *Applanopsis dampieri* (7.1-100), *Aquilapollenites* (4.1-8), *A. magnus* (7.1-100), *Aralaephyllum cachetamanense* (7.1-8), *Arapipia florifera* (7.1-97a), *Asterisporites asteroides* (7.1-3), *Auriculiidites reticulatus* (7.1-67, 68, 100), *Baculamonocolpites minimus* (7.1-80), *B. multispinosus* (7.1-80, 81, 82), *Baculamorphomonocolpites tausae* (7.1-80, 81, 82), *Baculatisporites multibaculae* (7.1-81), *Bahiaporites reticularis* (7.1-100), *Beaupreaidites* (7.1-55), *Bignonites chalianum* (7.1-8), *Buttinia andreevi* (7.1-100), *Carpinus subtriangula* (4.1-8), chenoam (?) (7.1-19), *Chilechicoxylon microporosum* (7.1-54), *Cinnamomum heeri* (7.1-8), *Circulina parva* (5.1-2), *Cissites parvifolius* (7.1-8), *Clatonipollenites* (?) (7.1-100), *Clavatipollenites* (7.1-5, 10, 99), *C. hughesii* (7.1-3, 55; see Incertae sedis below), *Com-*

plexipollis abditus (4.1-8), *Crassitricolporites brasiliensis* (7.1-100), *Cretaceioporites polygonalis* (7.1-78d), *Cricotriporites alamadaensis* (7.1-100), *C. guianensis* (7.1-100), *C. operculatus* (7.1-100), *Crototricolpites annemariae* (7.1-100), *Crusafontites grandiosus* (7.1-81, 82), *Cupaniedites reticularis* (7.1-100), *Cupuliferoidaepollenites* cf. *parvulus* (7.1-10), *C.* sp. (7.1-10), *Dorroteoxylon vicente-perezii* (7.1-54), *Echimonocolpites franciscoi* (7.1-94), *E. minutispinosus* (7.1-80), *Echiperiporites akanthos* (7.1-100), *E. estelae* (7.1-100), *Echitricolpites communis* (7.1-100), *E. polaris* (7.1-100), *Echitriporites triangulifor-mis* (7.1-100), *Elaterocolpites castelaini* (7.1-100), *Elateroplicites africaensis* (7.1-100), *Elateropollenites jardinei* (7.1-100), *Elaterosporites castelaini* (7.1-100), *E. klaszi* (7.1-100), *E. protensus* (7.1-100), *E. verrucatus* (7.1-100), *Endressiana brasiliana* (7.1-97a), *Ericipites* (7.1-80), *Escallonioxylon palaeoargutum* (7.1-54), *Extratriporopollenites firmis* (4.1-8), *E.* cf. *longianulus* (4.1-8), Fagaceae undet. (7.1-15; now Danian), *Fagus subferruginea* (7.1-15; now Danian [*Nothofagus*]), *Fenestrites gemmatus* (7.1-100), *Foveomorphomonocolpites* (*Proxapertites*) *humbertoides* (7.1-80, 81, 82), *Foveotricolpites* (7.1-74), *F. perforatus* (7.1-100), *Galeacornea causea* (7.1-100), *Gomortegoxylon patagonicum* (7.1-54), *Gonzalezoxylon mochaense* (7.1-54), *Hexaporotricolpites emelianovi* (7.1-100), *H. lamellaferus* (7.1-100), *H. potoniei* (7.1-100), *Hydrangea* (?) *incerta* (7.1-8), *Ilexpollenites* (4.1-8), *Inaperturopollenites crisopolensis* (7.1-74), *Jussitriporites* (7.1-100), *Kachikena compuesta* (7.1-text reference), *Laurelia* (7.1-9), *L. amarillana* (7.1-8), *Laurinium beilschmiedioides* (7.1-54), *Laurelioxylon intermedium* (7.1-54), *Laurinoxylon uniseriatum* (7.1-54), *Laurophyllum chalianum* (7.1-8), *L. hickenii* (7.1-8), *L. kurtzi* (7.1-8, 14), *L. proteaefolium* (7.1-8, 14), *Liliacidites* (7.1-10, 20, 74, 80, 99), *L. crassibaculatus* (7.1-16), *L. dividuus* (5.1-3), *L. variegatus* (7.1-16, 19, 55), *Liquidambar* [?] *integrifolium* (7.1-8), *Longapertites proxapertioides* (7.1-81, 100), *Magnaperiporites spinosus* (7.1-100), *Magnatriporites umirensis* (7.1-80), *Margotricolporites vanwijhei* (7.1-100), *Matayba marginatifolia* (7.1-15; now Danian), *Mauritidiites franciscoi* (7.1-65), *Menispermites obtusiloba* (7.1-8), *M. piatnitzkyi* (7.1-8, 14), *Momipites africanus* (7.1-100), *M. tenuipolus* (4.1-8), *Monocolpites* (7.1-100), *M. ruedae* (7.1-81), *Monocolpopollenites* (7.1-55, 99), *M. spheroides* (7.1-100), *Monocotylophyllum heterophyllum* (7.1-74), *Monoporites annulatus* (7.1-100), *Monosulcites* (5.1-2), *M. minutiscabratus* (7.1-19), *Multiareolites formosus* (7.1-100), *Multiporopollenites* aff. *maculosus* (7.1-100), *Myrceugenelloxylon pseudoapiculatum* (7.1-54), *Myrcia acutifolia* (7.1-8), *M. santacruzensis* (7.1-8, 14), *Myrica annulites* (4.1-8), *Myrtaceidites mesonensus* (7.1-16, 19), *Myrteoidea patagonica* (7.1-9), *Nelumbo puertae* (Upper Cretaceous, Chubut, Patagonia, Argentina; Gandolfo & Cúneo, 2005), *Nothofagidites* (7.1-55), *N. acromegacanthus* (7.1-13), *N.* cf. *asperus* (7.1-13), *N. cranwellae* (7.1-13), *N. dorotensis* (7.1-13), *N. fortispinulosus* (7.1-13), *N. fuegiensis* (7.1-13), *N. hystricosphaeroides* (7.1-13), *N. kaitangatus* (7.1-13), *N. paucispinosus* (7.1-13), *N. rocaensis* (7.1-13), *N. saraensis* (7.1-13), *N. suggatei* (7.1-13), *N.* cf. *visserensis* (7.1-13), *N.* cf. *waipawensis* (7.1-13), *Nothofagoxylon antarcticum* (7.1-54), *N. ohzauanum* (7.1-54), *N. pseudoobliqum* (7.1-54), *N. sclariforme* (7.1-54), *Nothofagus variabilis* forma *microphylla* (7.1-15; now Danian), *Nudopollis terminalis* (4.1-8), *N. thiergarti* (4.1-8), *Nyssapollenites* cf. *squamosus* (7.1-10), *Obispocaulis myriophylloides* (4.1-7), *Oculopollis baculotrudens* (4.1-8), *Paragonzareoxylon chilenomesozoicum* (7.1-54), *Paranymphaea proteaefolia* (7.1-8, 14), *Parvisaccites* (?) (7.1-100), *Peninsulapollis gillii* (7.1-20), *Pentapsis valdiviae* (7.1-100), *Perfotricolpites digitatus* (7.1-100), *Periretipollis spinosus* (7.1-100), *Perisyncolporites pokornyi* (7.1-100), *Peromonolites peroreticulatus* (7.1-100), cf. *Persea* (4.1-1), *Perseophyllum hauthalianum* (7.1-8), *Peumus clarki* (7.1-8), *Phymopollenites pannosus* (7.1-10), *P.* sp. (7.1-10), *Platanus* [?] *obtusiloba* (7.1-8), *Plicapollis bellus* (7.1-80), *P. serta* (4.1-8), *Populites lancastriensis* (7.1-8), *Populus* [?] cf. *nebrascensis* (7.1-8), *P.* cf. *microphylla* (7.1-8), *Porocolpollenites* (7.1-11), *Proteacidites* (4.1-8), *P. dehaani* (7.1-65, 80, 100), *P. longispinosus* (7.1-100), *P. minor* (7.1-55), *P. parvus* (7.1-19), *P. subscabratus* (7.1-19), *Proteoxylon patagonicum* (7.1-54), *Proxapertites cursus* (7.1-100), *P. facetus* (7.1-100), *Pseudoplicapollis longiannulata* (4.1-8), *Pseudovacuopollis* (4.1-8), *Psilamonocolpites inornatus* (7.1-94), *P. medius* (7.1-80, 94), *Psilaperiporites bolivensis* (7.1-65), *P. robustus* (7.1-100), *P. suarezi* (7.1-65), Psila/scabraticolpates (7.1-78d), *Psilastephanocolporites* (7.1-80), *P. fissilis* (7.1-100), *Psilastephanoporites brasiliensis* (7.1-100), *P. stellatus* (7.1-100), *Psilatetradites umirensis* (7.1-94), *Psilatricolpites* (7.1-20, 80, 99), *P. clarissimus* (7.1-94), *P. divisus* (7.1-65), *P. papilioniformis* (7.1-100), *P. patagonicus* (7.1-16, 19), *P. pulcherrimum* (7.1-16), *P. rubini* (7.1-94), *Psilatricolporites* (7.1-20), *P. crassus* (7.1-100), *P. florschutzi* (7.1-94), *P. maculosus* (7.1-100), *P. operculatus* (7.1-100), *P.* cf. *salamanquensis* (7.1-19), *P. triangularis* (7.1-100), *Quercus aurita* [?] (5.1-3), *Q.* [?] *primordialis* (7.1-8), *Retibrevitricolpites triangulatus* (7.1-100), Reticolates (7.1-78d), *Reticulatasporites jardinus* (7.1-99, 100), *Retidiporites magdalenensis* (7.1-80), *Retimonocolpites* (7.1-65, 78d), *R. dividuus* (7.1-74), *R.* aff. *Clavatipollenites minutus* (7.1-74), *R. peroreticulatus* (7.1-99), *Retimonoporites tequendamae* (7.1-94), *Retisyncolporites aureus* (7.1-80), *Retitricolpites* (5.1-2; 7.1-80), *R. amapaensis* (7.1-100), *R. americana* (7.1-100), *R. georgensis* (5.1-3), *R. letitiae* (7.1-94), *R. microreticulatus* (7.1-94), *R. retiaphelis* (7.1-65), *R. reticulatus* (7.1-94), *R. sphaeroides* (5.1-3), *R. vulgaris* (5.1-2; 7.1-74, 90), *Retitricolporites* (7.1-55, 80), *R. amazonensis* (7.1-100), *R. belmontensis* (7.1-100), *R. chubutensis* (7.1-19), *R. florschutzi* (7.1-94), *R. guianensis* (7.1-100), *R. irregularis* (7.1-100), *R. microreticulatus* (7.1-65), *R. perpusillus* (7.1-100), *R. quadrosi* (7.1-100), *R. reticulatus* (7.1-94), *R. squarrosus* (7.1-100), *Retitriporites mirabilis* (7.1-100), *Reyea polymorphus* (7.1-100), *Rhoipites* (7.1-16, 20), *R. baculatus* (7.1-19), *R. minusculus* (7.1-19), *Rogersia australis* (7.1-text reference), *Rollinia* (?) *patagonica* (7.1-8), *Rosannia manika* (7.1-19), *Rousea georgensis* (7.1-10), *Rouseisporites* (7.1-11), *Ruprechtia castilloensis* (7.1-8), *Salix* [?] *proteaefolia* (7.1-8), *Sassafras* [?] *acutilobum* (7.1-8), *S. cretaceum* (7.1-8), *S. mudgei* (7.1-8), *S. subintegrifolium* (7.1-8), *Scabraperiporites nativensis* (7.1-100), *Schinopsis* (?) *dubia* (7.1-8), *Scollardia trapaformis* (7.1-100), *Sinipites* (4.1-8), *Sofreipites* (7.1-65), *S. legouxae* (7.1-100), *Spinozonocolpites* (7.1-65), *S. baculatus* (7.1-81, 100), *S. echinatus* (7.1-81, 100), *Srivastapollenites exoticus* (7.1-19), *Stellatopollis* (7.1-74), *S. araripensis* (7.1-99), *Sterculia patagonica* (7.1-8), *S. sehuensis* (7.1-8, 14), *S. washburni* (7.1-8), *Striacolporites gamerroi* (7.1-19), *Striatricolpites* (7.1-65, 80), *S. catatumbus* (7.1-100), *Striatricolporites gamerroi* (7.1-19), *Striopollenites dubius* (7.1-100), *S. terasmaei* (7.1-100), *Syncolporites* (7.1-55), *S. poricostatus* (7.1-65), *S. triangularis* (7.1-100), *Tarahumara sophiae–Obispocaulis myriophylloides* (4.1-7), *Tetracolpites* (7.1-74), *Tetradites* (7.1-65,

100), *T. umirensis* (7.1-81), *Thorphyllum patagonia* (7.1-text reference), *Triatriopollenites bertelsii* (7.1-19), *T. excelsus* (4.1-8), *T. lateflexus* (7.1-19), *T. maedae* (7.1-55), *Tricesticillus americanus* (7.1-11), *Tricolpites* (7.1-11, 74), *T. gigantoreticulatus* (7.1-100), *T. gillii* (7.1-19), *T. microreticulatus* (7.1-55), *T. minutus* (7.1-10), *T. reticulata* (7.1-19), *T. retielegans* (7.1-16), *T. synstriatus* (7.1-65, 100), *T. tienabaensis* (7.1-100), *Tricolpollenites minutus* (5.1-3), *T. polyhedrus* (5.1-3), *Tricolpopollenites fallax* (7.1-55), *Tricolporites* (7.1-11, 16, 65), *Tricolporopollenites distinctus* (7.1-93), *T. microporifer* (7.1-55), *T. minor* (7.1-55), *T. punctulosus* (7.1-55), *Tricornites elongatus* (7.1-65, 100), *Trifossapollenites* (7.1-100), *Trifurcata flabellata* (7.1-97a), *Triorites* (7.1-65), *T.* cf. *minor* (7.1-16), *T. minusculus* (7.1-16), *Triporites* (7.1-80), *T. africaensis* (7.1-100), *T. iversenii* (7.1-81), *T. suescae* (7.1-81), *Triporopollenites* (7.1-11), *T. bituitus* (4.1-8), *T. coryloides* (4.1-8), *T. festatus* (7.1-55), *T. lateflexus* (7.1-20), *T. shimensis* (7.1-55), *Triporotetradites gemmatus* (7.1-65), *Trudopollis* cf. *ana(o)culus* (4.1-8), *T.* cf. *meckeri* (4.1-8), *Ulminium* (7.1-54), *Ulmoideipites krempii* (7.1-65, 100), *Vacuopollis* (4.1-8), *Verrustephanoporites simplex* (7.1-19), *Verrutricolpites* (7.1-10, 80), *Verrutricolporites* (7.1-80), *V. rotundiporus* (7.1-100), *Verrutriporites asymmetricus* (7.1-100), *Victorisporis* cf. *roberti* (7.1-100), *Zlivisporis blanensis* (7.1-100), *Zonocostites ramonae* (7.1-100). Incertae sedis: *Afropollis operculatus* (7.1-74), *Catinipollis geisaltalensis* (7.1-19), *Celyphus rallus* (7.1-3), *Chomotriletes minor* (7.1-5), *Cinnamomoides gachetaenis* (7.1-74), *Classopollis* (?) (7.1-80), *Clavatipollenites* (7.1-5), *C. hughesii* (5.1-3), *C. maximus* (5.1-3), *Cyclusphaera euribei* (7.1-67, 68), *Dicolpollis* (?) (7.1-80), *Dicotylophyllum* sp. (7.1-74), *Galeacornea* (5.1-3), *Microfasta evansii* (7.1-3), *Monosulcites* (7.1-74), *Moutonia quetamensis* (7.1-74), *M. sinuate* (7.1-74), *Mtchedlishvilia saltenia* (7.1-19), *Myrtoidea patagonica* (7.1-9), Palynomorph type A (5.1-3), *Phyllites* (7.1-74), *Retimonocolpites peroreticulatus* (7.1-74), *Schizosporis burcklei* (5.1-3), *S. reticulatus* (7.1-3), *Striatocolpites reticulatus* (7.1-74). Position unknown: *Confossia rara* (7.1-11), *C. vulgaris* (7.1-11), *Cuparieidites* (7.1-11), *Myrtoidea patagonica* (7.1-9), *Patera crassa* (7.1-11), *P. tenuis* (7.1-11), cf. *Reyrea* (7.1-74), *Schizosporis microreticulatus* (7.1-74).

Paleocene

(Includes some Late Cretaceous and late Paleocene–early Eocene occurrences)

Fungi

Ascomycetes (7.1-83), *Asterinites colombiensis* (7.1-83), *A. tellezii* (7.1-83), *Dicellaesporites* (7.1-31, 32, 34, 35), *D. fusiformis* (7.1-83), *D. magnus* (7.1-83), *D. rinconii* (7.1-83), *Diporisporites elongatus* (7.1-34, 35), *D. hammenii* (7.1-83), *Inapertisporites ovalis* (7.1-34, 35), *Lacrimasporonites arcuatus* (7.1-83), *L. ovalis* (7.1-83), *Monoporisporites perminutus* (7.1-83), *Multicellaesporites* (7.1-31, 32), *M. cerrejonensis* (7.1-83), *Pluricellaesporites* (7.1-34, 35), *Polyadosporites* (7.1-83).

Algae and allied groups

Catinipollis geiseltalensis (7.1-37), *Pediastrum* (7.1-31, 32).

Ferns and allied groups

Alsophilidites kerguelensis (7.1-56), *Apiculatisporis* (7.1-37), *Azolla* (7.1-37), *Baculatisporites* (7.1-34, 35, 37), *B. comaumensis* (7.1-56), *B. turbioensis* (7.1-29), *Biretisporites* (7.1-29, 37), *Cingutriletes australis* (7.1-29), *Clavifera triplex* (7.1-29), *Cyatheacidites* cf. *annulata* (7.1-29), *Cyathidites australis* (7.1-56), *C. minor* (7.1-29, 56), *C. patagonicus* (7.1-29), *Deltoidospora* (7.1-37), *Dictyophyllidites* (7.1-33), *D. concavus* (7.1-29), *Espora apiculada* (7.1-33), *Gabonisporis vigourouxii* (7.1-34, 35), *Gleicheniidites argentinus* (7.1-56), *G. circinidites* (7.1-56), *G. senonicus* (7.1-29), *Grapnelispora evansii* (7.1-37), *Ischyosporites* (7.1-37), *Laevigatosporites* (7.1-34, 35), *L. ovatus* (7.1-29, 56), *Leiotriletes regularis* (7.1-29), *Lycopodiumsporites austroclavatidites* (7.1-29), *Matonisporites* (7.1-29), *Neoraistrickia* (7.1-29), *Paleoazolla patagonica* (7.1-21), *Peromonolites* cf. *boweni* (7.1-56), *Retitriletes austroclavatidites* (7.1-34, 35), *Schizosporis paleocenicus* (7.1-56), *S. rugulatus* (7.1-56), *Triletes paravallatus* (7.1-29), *Tuberculatosporites parvus* (7.1-29).

Gymnosperms

Araucariacites australis (7.1-56), *Bororoa andreisii* (7.1-24), *B. anzulovichii* (7.1-24), *Cycadopites* (7.1-29), *C. adjectus* (7.1-56), *C. nitidus* (7.1-56), *Dacrydiumites florini* (7.1-56), *Ephedripites notensis* (7.1-56), *Inaperturopollenites* (7.1-34, 35), *Menucoa cazaui* (7.1-23), *Mesembrioxylon mazzonii* (7.1-24), *Microcachryidites antarcticus* (7.1-56), *Monosulcites minimus* (7.1-56), *Podocarpidites marwickii* (7.1-31–35), *P. otagoensis* (7.1-56), *Spheripollenites psilatus* (7.1-56), *Trisaccites microsaccatus* (7.1-56).

Angiosperms

Ailanthipites (7.1-31, 32, 37), *Akania americana* (7.1-25–27), *Albertipollenites angululuminosus* (7.1-29), *Anacolosidites diffusa* (7.1-29), *Annona* (7.1-25–27), *Banaraphyllum ovatum* (7.1-28), *Bombacacidites annaeoides* (7.1-95), *Bridelioxylon americanum* (7.1-24), *Callistopollenites* (7.1-30), *Caryophyllidites polyporatus* (7.1-56), *Casuarina* (7.1-25–27), *Casuarinidites coenozoicus* (7.1-56), *Cissites patagonica* (7.1-28), *Clavastephanocolporites ambigens* (7.1-95), *Clavatricolpites* cf. *gracilis* (7.1-31, 32, 37), *C. leticiae* (7.1-94), *Clavatricolporites leticiae* (7.1-95), *Cochlospermum* (7.1-25–27), *Confertisulcites* (7.1-29), *Corsinipollenites menendezii* (7.1-33, 37), *Cricotriporites guianensis* (7.1-33, 95), *Cristatricolpites analemae* (7.1-95), *Crototricolpites annemariae* (7.1-95), *Cryptocaryoides mariasantisimensis* (7.1-28), *Cupaneidites reticularis* (7.1-56), *Dryophyllum australis* (7.1-28), *Echimonocolpites franciscoi* (7.1-94), *E. ruedae* (7.1-84), *Echistephanoporites alfonsi* (7.1-33, 95), *Echitriporites guianensis* (7.1-94, 95), *Elaeocarpoxylon sloaneoides* (7.1-24), *Ephedripites* (7.1-31, 32, 37), *E. vanegensis* (7.1-84, 96; gymnosperm, Araceae), *Ericipites microtectatum* (7.1-30), *E. scabratus* (7.1-30), *Euxylophoroxylon chiquichanense* (7.1-24), Fagaceae indet. (7.1-15), *Fagophyllum duseni* (7.1-28), *Favitricolporites australis* (7.1-29), *Foveostephanocolpites perfectus* (7.1-94–96), *F. typicus* (7.1-95), *Foveostephanocolporites liracostatus* (7.1-95), *Foveotricolpites perforatus* (7.1-84), *F. pomarius* (7.1-84), *F. santanderianus* (7.1-84), *Gemmamonoclopites gemmatus* (7.1-84), *Gemmastephanocolpites*

asteroformis (7.1-94, 95), *Gemmatricolpites subsphaericus* (7.1-29, 31, 32, 37), *G. vigdisae* (7.1-95, 96), *Gemmatricolporites berbicensis* (7.1-95, 96), *G. divaricatus* (7.1-94, 95), *Haloragacidites harrisii* (7.1-29), *Heterocolpites palaeocenicus* (7.1-84, 96), *Jussitriporites menendezii* (7.1-34, 35), *Laurophyllum* (*Nectandra*) *chubutensis* (7.1-28), *L.* (*Oreodaphne*) *piatnitzkyi* (7.1-28), *Liliacidites kaitangataensis* (7.1-56), *L. regularis* (7.1-29, 30), *L. variagatus* (7.1-29, 37), *L. vermireticulatus* (7.1-30), *Liquidambarpollenites* cf. *brandonensis* (7.1-34, 35, 37; *Liquidambar* [?]), *Lomatia bivascularis* (7.1-25–27), *Longapertites andreisii* (7.1-29), *L. patagonicus* (7.1-29), *L. proxapertitoides* (7.1-84), *Magnotetradites magnus* (7.1-84), *Malvacipollis diversus* (7.1-56), *Matayba marginatifolia* (7.1-15), *Mauritiidites franciscoi* (7.1-84, 96), *Monosulcites minutiscabratus* (7.1-29), *Myrica premira* (7.1-28), *Myriophyllumpollenites* (7.1-31, 32, 37), *Myrtaceidites eugenioides* (7.1-56), *Nypa pernambucensis* (7.1-97b), *Nothopollenites* (7.1-34, 35), *Palmocarpon* (7.1-24), *Palmoxylon* (7.1-24), *P. patagonicum* (7.1-22), *Pandaniidites* (7.1-29), *P. texus* (7.1-31, 32, 37), *Paranymphaea aristolochiaformis* (7.1-28), *Peumus* (7.1-25–27), *Polyplicadites vanegensis* (7.1-94), *Polyporina romeroi* (7.1-29), *Proteacidites* (7.1-29), *P. amolosesinus* (7.1-56), *P. crassus* (7.1-56), *P. parvus* (7.1-56), *Proxapertites cursus* (7.1-96), *P. operculatus* (7.1-29, 84, 94, 96), *P. tertiaria* (7.1-84), *Psilamonocolpites inornatus* (7.1-94), *P. medius* (7.1-56, 84, 94, 96), *Psilastephanocolpites maia* (7.1-95, 96), *Psilastephanocolporites fissilis* (7.1-56, 95), *Psilatricolpites* (7.1-20), *P. acerbus* (7.1-37), *P. coprosmoides* (7.1-56), *P. fissilis* (7.1-56), *P. inargutus* (7.1-29), *P. minutus* (7.1-56), *P. palaeocenica* (7.1-84), *P. psilascabratus* (7.1-29), *P. simplex* (7.1-37), *P. solus* (7.1-95, 96), *P. undamaginis* (7.1-95), *Psilatricolporites* (7.1-29, 56), *P. salamaquensis* (7.1-30), *Restioniidites* (7.1-37), *R. pascualii* (7.1-29), *Retibrevitricolpites retibolus* (7.1-95), *Retidiporites botulus* (7.1-94–96), *R. camachoi* (7.1-29), *R. magdalenensis* (7.1-84, 94, 96), *Retimonocolpites microreticulatus* (7.1-84), *R. proxaperturoides* (7.1-94), *R. regio* (7.1-84), *Retistephanocolpites angeli* (7.1-94–96), *R.* cf. *guaduensis* (7.1-94), *Retitricolpites agricaulis* (7.1-95), *R. analemae* (7.1-94), *R. cecryphalium* (7.1-94–96), *R. herrerae* (7.1-84), *R. kwakwaniensis* (7.1-94, 95), *R. microreticulatus* (7.1-56, 84), *R. retiaphelis* (7.1-95, 96), *Retitricolporites* (7.1-31, 32), *R. annae* (7.1-84), *R. annaeoides* (7.1-84, 94), *R. chubutensis* (7.1-29, 30, 37), *R. costatus* (7.1-95, 96), *R. hispidus* (7.1-94), *R. mariposus* (7.1-95, 96), *R. medius* (7.1-33), *R. retiaphelis* (7.1-96), *Retitriporites retibolus* (7.1-94), *Rhizophoroxylon spallettii* (7.1-24), *Rhoipites* (7.1-34, 35, 37), *R. baculatus* (7.1-29, 37), *R. minusculus* (7.1-29, 31–33, 37), *Roupala patagonica* (7.1-25–27), *Rousea microreticulata* (7.1-30), *R. minuscula* (7.1-30), *R. patagonica* (7.1-29, 33, 37), *Rugutricolporites felix* (7.1-56), *Sabalpollenites* (7.1-29), *Scabrastephanocolpites lisamae* (7.1-84), *S. scabratus* (7.1-84), *S. vanegensis* (7.1-84), *Scabratriporites suescae* (7.1-94), *Schinopsis* (7.1-25–27), *Schizosporis paleocenicus* (7.1-56), *S. rugulatus* (7.1-56), *Senipites tercrassata* (7.1-29), *Smilacipites saltensis* (7.1-34, 35), *Sparganiaceapollenites* (7.1-29), *Spinozonocolpites* (7.1-29, 37), *S. hialinus* (7.1-30), *Srivastavapollenites exoticus* (7.1-36), *Stephanocolporites ambigens* (7.1-94), *Sterculia acuminataloba* (7.1-28), *Striatopollis exiguus* (7.1-30), *Striatricolporites gamerroi* (7.1-29), *S. pimulis* (7.1-95, 96), *Syncolporites lisamae* (7.1-84, 94, 95), *Syndemicolpites petriellai* (7.1-29), *Tiliaepollenites notabilis* (7.1-56), *Triatriopollenites bertelsii* (7.1-29), *T. lateflexus* (7.1-29), *Tricolpites bibaculatus* (7.1-30, 37), *T. communis* (7.1-29, 37), *T. gillii* (7.1-29), *T. lumbrerensis* (7.1-34, 35), *T. reticulata[-us]* (7.1-29, 33–35, 37), *T. vulgaris* (7.1-34, 35), *Triorites* (7.1-33), *T. edwardsii* (7.1-56), *T. harrisii* (7.1-56), *T. minor* (7.1-56), *T. minutipori* (7.1-56), *Ulmoideipites patagonicus* (7.1-29), *Verrucolporites giokina* (7.1-96), *Verrustephanocolpites verrucatus* (7.1-84), *Verrustephanoporites simplex* (7.1-31–35, 37, 95, 96), *Verrusyncolporites lisamae* (7.1-94), *Verrutricolpites giokina* (7.1-95), *V. isolatus* (7.1-95), *V. verrubolus* (7.1-95, 96), *Weinmannioxylon multiperforatum* (7.1-24), *W. pluriradiatum* (7.1-24), *Zizyphus chubutensis* (7.1-28). Incertae sedis: *Catinipollis geiseltalensis* (7.1-30, 37), *Curvimonocolpites inornatus* (7.1-95), *Dryoxylon* (7.1-24), *Mtchedlishvilia saltenia* (7.1-31, 32).

Eocene, some late Paleocene, Eo–Oligocene

Fungi

Dicellaesporites (7.1-59, 61, 64), *Didymoporisporonites* (7.1-61), *Dyadosporonites annulatus* (7.1-45), *Granatisporites* (7.1-59, 61, 64), *Inapertisporites* (7.1-59, 61, 64), *Lacrimasporonites* (7.1-45, 59, 61, 64), *Monoporisporites* (7.1-59, 61, 64), *Multicellaesporites* (7.1-59, 61, 64), *Plochmopeltinites masonii* (7.1-45), *Pluricellaesporites* (7.1-59, 61, 64), *P. psilatus* (7.1-45).

Algae

Botryococcus braunii (7.1-46, 61), *Catinipollis geiseltalensis* (7.1-47), *Chomotriletes* (7.1-91), *Chondrites subsimplex* (7.1-58), *Micrast[h]erias* (7.1-91), *Mougeotia* sp. (7.1-47), *M.* cf. *laetivirens* (7.1-47), *Operculodinium* (7.1-91), *Pediastrum* (4.1-10; 7.1-66), *Spirogyra* (7.1-47), *Zygnema* (7.1-47).

Bryophyta

Cingutriletes australis (7.1-42, 46), *Reboulisporites fuegiensis* (7.1-47), *Sphagnum* (?) (7.1-59).

Ferns and allied groups

Adianites borgoniana (7.1-58), *Apiculatasporites* (?) *cingulatus* (7.1-85), *A. obscurus* (7.1-85), *Appendicisporites* (4.1-10), *Asplenium* (7.1-15), *A. incertum* (7.1-41), *Baculatisporites* (7.1-85), *B. comaumensis* (7.1-42, 46, 47), *B. turbioensis* (7.1-42, 46), *Biretisporites crassilabratus* (7.1-42, 46), *Blechnum* (7.1-57), *B. antediluvianum* (7.1-58), *Camarozosporites* (4.1-10; 7.1-85), *Ceratopteris* (6.1-2), *Chomotriletes fragilis* (7.1-66), *C. minor* (7.1-85), *Cicatricosisporites* (4.1-10), *C. dorogensis* (7.1-85), *Cicatricoso[i]sporites decussatus* (7.1-85), *C. eocenicus* (7.1-85), *Cingutriletes australis* (7.1-42, 46), *Clavatisporites mutisii* (7.1-85), *Clavifera* (7.1-59, 64), *Concavisporites* (7.1-42), *C.* cf. *stavensis* (5.1-5), *Corrugatisporites argentinus* (7.1-42, 46), *Cyatheacidites annulatus* (7.1-42, 46, 60), *Cyathidites australis* (7.1-59, 61), *C. minor* (7.1-42, 46, 59, 61, 64), *C. patagonicus* (7.1-42, 61), *Cyathoides thyrsopterioides* (7.1-58), *Deltoidospora* (5.1-7a; 7.1-42, 66), *D. minor* (4.1-11), *Dicksonia patagonica* (7.1-41), *Echinatisporis* cf. *aculeatus* (4.1-10), *Echinatisporites* (4.1-11), *E. brevispinosus* (7.1-85), *Echitriletes mulleri* (7.1-66), *Filicites* (7.1-15), *Foveotriletes margaritae* (7.1-85), *F. palaequetrus* (7.1-46), *Gleicheniidites* (7.1-59, 64), *G. senonicus* (7.1-42, 66), *Goniopteris patagoniana* (7.1-41), *Intrapunctosporis semipunctus* (7.1-87),

Ischyosporites problematicus (7.1-85), *Kirchheimerisporites tenuiradiatus* (7.1-85), *Laevigatosporites* (5.1-7; 7.1-59, 64, 85), *L. discordatus* (7.1-87), *L. haardtii* (5.1-5), *L. nutidus* (7.1-87), *L. ovatus* (7.1-42, 46), *L. tibuensis* (7.1-85), *L. vulgaris* (7.1-61), *Leiotriletes* (7.1-59, 64), *L. regularis* (7.1-42), *Leptolepidites densus* (7.1-42), *Lycopodiumsporites austroclavatidites* (7.1-42, 46), *L. eminulus* (7.1-42, 47), *L. novomexicanum* (7.1-66), *Lygodiumsporites adriennis* (4.1-9; 5.1-5, 7), *Microfoveolatosporis skottsbergii* (7.1-85), monolete fern spores (6.1-2), *Muricingulisporis chenquensis* (7.1-46), *Ornatisporites* aff. *dentatus* (5.1-5), *Osmundacidites* (7.1-66), *O. minor* (7.1-85), *Pecopteris* (7.1-15), *P. buhsei* (7.1-58), *Peromonolites* (7.1-42, 59, 64), *P. vellosus* (7.1-46), *Perotriletes* (7.1-66), *Planisporites* (7.1-85), *Polypodiaceoisporites* (?) *fossulatus* (7.1-85), *P. potoniei* (7.1-66), *Polypodiidites speciosus* (7.1-42), *Polypodiisporites* (7.1-46, 91), *Polypodiisporonites alienus* (5.1-5), *P. echinatus* (7.1-85), *P.* cf. *favus* (5.1-5), *P.* aff. *inangahuensis* (7.1-85), *P. pachyexinatus* (7.1-85), *P.* aff. *speciosus* (7.1-85), *Polypodium* type (7.1-61), *Pteridacidites* (7.1-85), *Pteris* (6.1-2), *P. cousiniona* (7.1-58), *P. dentata* (4.1-9; 5.1-7), *P. frenguellii* (7.1-15), *Reticuloidosporites* cf. *tenellis* (7.1-42), *Retitriletes* (7.1-85), *Scabramonoletes* (?) (7.1-85), *Selaginella* (4.1-9; 6.1-2), *Sphaeropteris–Trichipteris* (6.1-2), *Sphaen[r]opteris molinae* (7.1-15), *Stereisporites crassiancoris* (4.1-10), *S. microgranulus–crassiexinus* (4.1-10), trilete fern spores (5.1-7; 6.1-2), *Triletes* (7.1-60), *T. fasolae* (7.1-42), *T. parvallatus* (7.1-42, 46), *Triletes tuberculiformis* (7.1-60), *Tuberculatosporites parvus* (7.1-42), *Tuberositriletes verrucatus* (7.1-85), *Undulatisporites concavus* (5.1-7), *Verrucatosporites favus* (4.1-10), *V. megafavus* (4.1-10), *V. usmensis* (5.1-7; 7.1-66, 87), *Verrucosisporites* (7.1-61), *Woodwardia* (7.1-15), *Zlivisporis blanensis* (7.1-85).

Gymnosperms

Abietineaepollenites (4.1-11), *Acmopyle engelhardti* (7.1-15), *Araucaria* (7.1-15), *A. araucoensis* (7.1-58), *A. nathorsti* (7.1-15), *A. pichileufensis* (7.1-41), *Araucariacites* (7.1-59, 85), *A. australis* (7.1-43, 46, 61, 66), *Ca(o)rollina torosus* (4.1-11), *Cedripites* (4.1-11; 7.1-66), *Dacrycarpites australiensis* (7.1-43), *Dacrydiumites florinii* (7.1-43), *Ephedra* (7.1-58), *Ephedripites vanegensis* (7.1-85), *Equisetosporites notensis* (7.1-43), *Fitzroya tertiaria* (7.1-41), *Gamerroites psilasaccus* (7.1-46), *Ginkgo patagonica* (7.1-41), *Libocedrus prechilensis* (7.1-41), *Lygistepollenites florinii* (7.1-46), *Microcachrydites antarcticus* (7.1-43), *Phyllocladidites mawsonii* (7.1-43, 46, 47, 60), *P. ruei* (7.1-43), *P.* cf. *verrucosus* (7.1-46), *Podocarpidites* (7.1-59, 64, 66), *P. elegans* (7.1-43, 46), *P. ellipticus* (7.1-46), *P.* cf. *exiguus* (7.1-46), *P. magnus* (7.1-43), *P. marwickii* (7.1-43, 61), *P. microreticuloidata* (7.1-43), *P.* cf. *otagoensis* (7.1-61), *P. rugulosus* (7.1-43, 46), *Podocarpus andiniformis* (7.1-41), *P. engelhardti* (7.1-41), *P. inopinatus* (7.1-57), *Pristinuspollenites* (4.1-11), *Sequoia chilensis* [?] (7.1-58), *Trisaccites* (7.1-59), *T. microsaccatum* (7.1-43, 46, 61), *Zamia tertiaria* (7.1-41, 58).

Angiosperms

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41), *Cordia pulchra* (7.1-58), *C. vera* (7.1-77), *Corsinipollenites* (5.1-7a), *C. psilatus* (7.1-85), *C. undulatus* (7.1-85), *Coussapoa prepliocenica* (7.1-15), *C.* (?) *quinquenervis* (7.1-58), *Coussarea membranacea* (7.1-58), *C. tertiaria* (7.1-41), *Crassiorites australis* (7.1-47), *Cricotriporites elongatoporus* (7.1-85), *C. guianensis* (7.1-85), *C. macroporus* (7.1-85), *C. minutiporus* (7.1-85), *Crototricolpites americanus* (7.1-96), *C.* cf. *annemariae* (7.1-85), *C. protoannemariae* (7.1-85), *Crudia* (6.1-2), *Crusafontites megagemmatus* (7.1-85), *Cryptocarya* (7.1-57), *Ctenolophonidites cruciatus* (7.1-85), *Cucurbites compressus* (7.1-70), *Cupaneidites* (5.1-7a; 7.1-59, 64), *Cupania cordinii* (7.1-41), *C. grosse-serrata* (7.1-15, 41), *C. latifolioides* (7.1-15, 41), *C. patagonica* (7.1-15, 41), *C. romeroi* (7.1-57), *C. vernaliformis* (7.1-15, 41, 57), *C.* sp. (7.1-15), *Cupanoides peruvianus* (7.1-69, 70), *Cupuliferoi[dae]pollenites* (4.1-10), *C. liblarensis* (5.1-7), *Curvimonocolpites inornatus* (7.1-85), *Dalbergia patagonica* (7.1-41), *Desmodium obliquim* (7.1-58), *Diatenopteryx fossilis* (7.1-41), *D. sorbifoliforma* (7.1-41), *Diporites* (7.1-59, 64), *Doliocarpus oblongifolia* (7.1-58), *D.* (?) *serrulata* (7.1-58), *Drimys patagonica* (7.1-15, 41), *Dryophyllum australis* (7.1-15), *Duplotriporites ariani* (7.1-85), *Echimonocolpites* (7.1-85), *E. densus* (7.1-86), *Echimorphomonocolpites gracilis* (7.1-86), *E. solitarius* (7.1-86), *Echiperiporites akanthos* (7.1-66), *E. estelae* (7.1-66, 85), *Echinostephanocolpites echinatus* (7.1-96), *Echistephanoporites alfonsi* (7.1-94), *Echites tertiaria* (7.1-41), *Echitetracolpites* (?) *tenuiexinatus* (7.1-85), *Echitricolpites* (5.1-7; 7.1-85), *Echitriporites guianensis* (7.1-96), *E. trianguliformis* (7.1-85, 86, 91), *E. variabilis* (7.1-85), *Embothriophyllum dubium* (7.1-38), *Embothrium precoccineum* (7.1-41), *E. pregrandiflorum* (7.1-41), *Empedoclea repando-serrata* (7.1-58), *Ericipites* (7.1-44), *E. annulatus* (7.1-86), *Erythrochiton borrelloensis* (7.1-15), *E. grandifolium* (7.1-58), *Erythroxylon cuneifolioides* (7.1-41), *E. reichei* (7.1-58), *Escallonia frenguellii* (7.1-15), *Eucryphia tertiaria* (7.1-41), *Eugenia–Myrcia* (6.1-2), *Extratriporopollenites* (4.1-10), *Fagara piurana* (7.1-70), *F. serrata* (7.1-41), *Fagophyllum duseni* (7.1-15), *Fagus* [?, *Nothofagus*] *dicksoni* (7.1-15, 38), *F. integrifolia* (7.1-38), *F. morenoi* (7.1-15), *F. obscura* (7.1-15), *F. subferrusinea* (7.1-15, 38), *Faramea* (6.1-2), cf. *Ficus* (6.1-2), *F. americanafolia* (7.1-89), *F. patagonica* (7.1-41), *F. sphericus* (7.1-70), *Foveodiporites guianensis* (7.1-85), *Foveostephanocolpites typicus* (7.1-96), *Foveotricolpites genuinus* (7.1-86), *F. perforatus* (7.1-85), *Foveotricolporites caldensis* (7.1-86), *F. fossulatus* (7.1-85), *F. marginatus* (7.1-86), *F. rugulatus* (7.1-85), *F. voluminosus* (7.1-86), *Foveotriporites hammenii* (7.1-85, 86), *Fraxinopollenites* cf. *scoticus* (5.1-7), *Gaultheria* (7.1-57), *Gemmamonocolpites amicus* (7.1-86), *G. barbatus* (7.1-86), *G. gemmatus* (7.1-85), *G. ovatus* (7.1-86), *G. perfectus* (7.1-85), *Gemmastephanoporites breviculus* (7.1-86), *G. polymorphus* (7.1-86), *Gemmatricolpites pulcher* (7.1-86), *G. vigdisae* (7.1-96), *Goeppertia* (7.1-15), *G. engelhardti* (7.1-58), *G. ovalifolia* (7.1-41, 58), *G. spectabilis* (7.1-58), *Gothanipollis bassensis* (7.1-45), *Gouatteria tenuinervis* (7.1-58), Gramineae type (7.1-96), *Graminidites* (4.1-11), *G. gramineoides* (5.1-5, 7), *Guazuma* (7.1-15), *Haemadictyon tenuifolium* (7.1-58), *Haloragacidites harrisii* (7.1-59, 64), *Heterocolpites paleocenicus* (7.1-96), *H. paluster* (7.1-86), *Hoffmannia protogaea* (7.1-41, 58), *Horniella* (7.1-85), *Hydrangea incerta* (7.1-15, 41), *Icica pichileufuana* (7.1-41), *Ilex* (6.1-2), *I. subtilinervis* (7.1-58), *Ilexpollenites auriculoides* (4.1-10), *I. clifdenensis* (7.1-45), *Inga eolaurina* (7.1-88), *I. patagonica* (7.1-41), *Intratriporopollenites* (7.1-44), *Iriartites* (7.1-58), *I. restinensis* (7.1-71), *Jandufouria minor* (7.1-85), *Janmulleripollis pentaradiatus* (7.1-92), *Jatropha tertiaria* (7.1-70), *Juglans* [?] *licciardoensis* (7.1-15), *Jussitriporites* (4.1-10; 7.1-66), *J. undulatus* (7.1-86), *Ladakhipollenites rubinii* (7.1-85), *L. simplex* (7.1-85), *Laetia transversinervis* (7.1-58), *Lakiapollis* aff. *ovatus* (7.1-85), *Lanagiopollis crassa* (7.1-85), *L. eocaenica* (4.1-9), *Landolphia paraparaensis* (7.1-41), *Laurelia guinazui* (7.1-15, 41), *L. insularis* (7.1-15), *Laurophyllum actinodaphnoides* (7.1-15, 58), *L.* sp. (7.1-15), *Lecythis* (7.1-15), *L. neriifolia* (7.1-58), *Leea* (4.1-9), *Leguminosites* (7.1-57), *L. belensis* (7.1-70), *L. copaiferaeoides* (7.1-58), *L. erythrinoides* (7.1-58), *L. mucunoides* (7.1-69, 70), *Leptolobium prenitens* (7.1-41), *Liliacidites* (5.1-7), *L. complexus* (4.1-10), *L. intermedius* (5.1-5), *L. variegatus* (4.1-10), *Lisianthius* (6.1-2), *Lithospermites glabrum* (7.1-70), *Lomatia* (7.1-15), *L. preferruginea* (7.1-41), *L. serrulata* (7.1-15), *Longapertites brasiliensis* (7.1-86), *L. circulatus* (7.1-86), *L. fossuloides* (7.1-86), *L. microfoveolatus* (7.1-85), *L. perforatus* (7.1-86), *L. proxapertitoides* (7.1-85, 86), *Longitrichotomocolpites triangularis* (7.1-86), *Luehea divaricatiformis* (7.1-98), *Luminidites colombianensis* (7.1-85), *Lymingtonia* (?) (7.1-85), *L.* cf. *rhetor* (5.1-7), *Magnaperiporites spinosus* (7.1-86), *Magnatriporites abstractus* (7.1-86), Malpighiaceae (6.1-2; 7.1-96), *Malvacarpus guinazui* (7.1-41), *M. octoloculus* (7.1-70), Malvaceae type [?] (7.1-61), *Malvacipollis argentina* (7.1-47), *M. tschudyi* (5.1-7), *Margocolporites vanwijhei* (7.1-66, 85), *Mascagnia sepiumoides* (7.1-41), *Matayba belensis* (7.1-70), *M. marginatifolia* (7.1-15, 41), *Mauritiidites* (5.1-7a; 7.1-91), *M. franciscoi* (7.1-85, 87, 96), *Maytenus araucensis* (7.1-58), *M. ellipticus* (7.1-41), *M. latifolioides* (7.1-41), *M. magnoliaefolia* (7.1-58), *Melastomaceophyllum danielis* (7.1-78a), *Mespilodaphne longifolia* (7.1-15, 58), *Milfordia minima* (7.1-66), *Momipites* (4.1-10), *M. africanus* (7.1-85), *M. corylipites* (4.1-11), *Momisia* (7.1-15), *M. australis* (7.1-41), *Monocolpites* (7.1-61, 66), *M. medius* (7.1-87), *Monocolpopollenites* (4.1-10), *M. ovatus* (7.1-85), *M.* aff. *tranquillus* (5.1-5), *Monocolporites* (4.1-10), *Monoporites annulatus/annuloides* (7.1-66, 86), *Monoporopollenites annulatus* (7.1-85), *Monosulcites* (7.1-59), *Monstera marginiata* (7.1-98), *Mortoniodendron* (6.1-2), *Moschoxylun falcatum* (7.1-58), *M. tenuinerve* (7.1-58), *Multiporopollenites pauciporatus* (7.1-85), *Myrceugenia tertiaria* (7.1-41), *Myrcia chubutensis* (7.1-15, 41), *M. costatoides* (7.1-58), *M. deltoidea* (7.1-40, 41, 57, 58), *M. nitens* (7.1-58), *M. obovata* (7.1-41), *M. reticulato-venosa* (7.1-15, 41, 58), *M.* cf. *rostrataformis* (7.1-98), *Myrciaria acuminata* (7.1-58), *Myrciophyllum ambiguaeoides* (7.1-58), *Myrica mira* (7.1-41), *M.* [?] *premira* (7.1-15), *Myristica fossilis* (7.1-15, 41, 58), Myrtaceae (7.1-96), *Myrtaceidites* (7.1-59, 61, 64), *M.* cf. *parvus* (5.1-7), *M. verrucosus* (7.1-44, 46), *Myrtiphyllum bagualense* (7.1-57), *Nectandra* cf. *antillanafolia* (7.1-88), *N. chilana* (7.1-15, 58), *N. patagonica* (7.1-41), *N. prolifica* (7.1-15, 41, 57), *Nothofagidites acromegacanthus* (7.1-46), *N. asperus* (7.1-43), *N. brachispinulosa* (7.1-43), *N. cincta* (7.1-43, 61), *N. cranwellae* (7.1-43), *N. deminuta* (7.1-43), *N. dorotensis* (7.1-46), *N. fortispinulosus* (7.1-43), *N. huertasii* (7.1-85), *N. mensiesii* group (7.1-61), *N. micromarginata* (7.1-43), *N. nana* (7.1-43), *N. saraensis* (7.1-43, 46), *N. suggatei* (7.1-47), *N. tehuelchesii* (7.1-46), *Nothofagus* (4.1-11), *N. australis* (7.1-15), *N. brassii* group (7.1-60), *N. densi-nervosa* (7.1-15), *N. elongata* (7.1-

15, 38), *N. fusca* group (7.1-60), *N. lanceolata* (7.1-15), *N. magellanica* (7.1-15), *N. pulchra* (7.1-15), *N. serrulata* (7.1-15), *N. simplicidens* (7.1-15), *N. variabilis* (7.1-38), forma *microphylla* (7.1-15), forma *oblonga* (7.1-15), *Notophoebe neogaea* (7.1-15, 41), *N. ovatifolia* (7.1-15, 41), *Nudopollis terminalis* (4.1-10), *Nyctaginites ellipticus* (7.1-41), *Omphales[a] filiciformis* (7.1-15, 58), *O. flaviana* (7.1-15), *O. patagonica* (7.1-41), *Oreodaphne piatnitzkyi* (7.1-15), *O. preacutifolia* (7.1-41), *Oreopanax guinazui* (7.1-41), *Ouratea firmifolia* (7.1-41, 58), *Paleosantalaceaepites distinctus* (7.1-85), Palmae (6.1-2; 7.1-96), Palm (rays) (7.1-88), *Palmocarpon belensis* (7.1-70), *P. bravoi* (7.1-69, 70, 72), *P. cocoides* (7.1-70), *Papillamonocolpites splendens* (7.1-86), *Papillopollis partialis* (7.1-86), *Paragonia–Arrabidaea* (6.1-2), *Parani[y]mphaea patagonica* (7.1-15), *Paraoreomunnea* (4.1-9), *Parsonsidites* (7.1-85), *P. conspicuous* (4.1-11), *Patrisia eocenica* (7.1-15, 58), *Paullinia* (6.1-2), *P. prerufescens* (7.1-41), *P. rubiginosifolia* (7.1-41), *Pelliceria* (6.1-2), *Pellicieroipollis* (4.1-11), *Perfotricolpites digitatus* (7.1-85, 86), *P. semistriatus* (7.1-86), *Pericolporites* (5.1-7), *Periporopollenites demarcatus* (7.1-44), *Periretisyncolpites giganteus* (7.1-85), *Perisyncolporites pokornyi* (7.1-85), *Persea macrophylloides* (7.1-58), *P. microphylla* (7.1-15, 58), *Phoebe elliptica* (7.1-41, 57, 58), *P. lanceolata* (7.1-15, 41, 58), *Pilocarpus saavedrai* (7.1-58), *Platanus* [?] *patagonica* (7.1-15), *Platycarya swasticoida* (4.1-10), *Plicapollis arcii* (7.1-86), *Plumiera articulatifolia* (7.1-41), *Poacidites* (7.1-38), *P. chloriformis* (7.1-41), *Polioexolobus molinae* (7.1-15), *P. prenuntius* (7.1-41), *Poloretitricolpites absolutus* (7.1-85), *Polotricolporites concretus* (7.1-86), *P. mocinii* (7.1-86), *P. versabilis* (7.1-86), *Polylepis prenuntia* (7.1-41), *Polyporina* (7.1-59), *Porocolpopollenites* (5.1-7), *Pouterlabatia clarki* (7.1-15, 41), *P. lanceolata* (7.1-15, 41), *Propylipollis pseudocostatus* (7.1-85), Proteaceae (7.1-60), *Proteacidites* (7.1-46, 59, 61, 64), *Protium* (6.1-2), *Proxapertites* (4.1-10), *P. cursus* (7.1-85, 96), *P. humbertoides* (7.1-85), *P. magnus* (7.1-85), *P. operculatus* (7.1-85, 96), *P. psilatus* (7.1-85), *P. verrucatus* (7.1-85), *Pseudostephanocolpites perfectus* (7.1-86), *P.* (?) *verdi* (7.1-86), *Pseudowinterapollis couperi* (7.1-46), *Psidium araciforme* (7.1-15, 41), *P. membranaceum* (7.1-58), *P. paulense* (7.1-98), *Psilabrevitricolpites* (7.1-85), *Psilabrevitricolporites simpliformis* (7.1-85), *P. triangularis* (7.1-85), *Psiladiporites guianensis* (7.1-94), *P. redundantis* (5.1-7; 7.1-86), *Psilamonocolpites* (7.1-59, 64), *P. grandis* (7.1-85), *P. medius* (7.1-85, 96), *Psilaperiporites* (7.1-91), *P. minimus* (7.1-66), *P. robustus* (7.1-66), *Psilastephanocolpites* (7.1-85), *P. adinos* (7.1-86), *P. fissilis* (7.1-94), *P. marginatus* (7.1-86), *P. verrucosus* (7.1-86), *Psilastephanocolporites brevicolpatus* (7.1-85), *P. fissilis* (7.1-85), *Psilastephanoporites* (7.1-85), *Psilasyncolporites* (7.1-85), *P. parvus* (7.1-86), *Psilatricolpites* (7.1-66), *P. acerbus* (7.1-86), *P. brevis* (7.1-86), *P. ciliatus* (7.1-96), *P. hirsutus* (7.1-96), *P. minutus* (7.1-86, 96), *P. polaroides* (7.1-86), *P. simplex* (7.1-86), *P. solus* (7.1-94), *Psilatricolporites* (7.1-59), *P. amagensis* (7.1-87), *P. cereus* (7.1-96), *P. crassus* (5.1-7a; 7.1-91, 96), *P. maculosus* (7.1-66), *P. molinae* (7.1-87), *P. normalis* (7.1-86), *P. obscurus* (7.1-86), *P. operculatus* (7.1-66, 86, 91), *P. optimus* (7.1-86), *P. rotundisprus* (7.1-96), *P. triangularis* (7.1-96), *P. vanus* (7.1-86), *Psilodiporites redundantis* (5.1-7), *Psittacanthus crassifolius* (7.1-58), *Psychotria eogenica* (7.1-70), *grandifolia* (7.1-58), *Quercus* [?] *angustiloba* (7.1-15), *Racemonocolpites facilis* (7.1-85, 86), *R. racematus* (7.1-85, 86), *R. romanus* (7.1-86), *Ranunculacidites operculatus* (7.1-85), *Rapanea* (7.1-57), *Remijia tenuiflorifolia* (7.1-41), *Retibrevitricolpites* (5.1-7), *R. catatumbus* (7.1-86), *R. increatus* (7.1-86), *R. retibolus* (7.1-85), *R. triangulatus* (7.1-85, 86, 91), *Retibrevitricolporites* (5.1-7), *R. grandis* (7.1-85), *R. speciosus* (7.1-85), *Reticulataepollis* cf. *intergranulata* (5.1-7), *Retidiporites agilis* (7.1-86), *R. botulus* (7.1-96), *R. elongatus* (7.1-85), *R. magdalenensis* (7.1-85), *R. poricostatus* (7.1-85), *Retiheterocolpites tertiarius* (7.1-86), *Retimonocolpites* (5.1-7, 7a), *R. bernardii* (7.1-86), *R. splendidus* (7.1-86), *R. tertiarius* (7.1-86), *Retipollenites* (7.1-85), *R.* cf. *confusus* (5.1-7), *Retistephanocolpites angelicus* (7.1-85, 86), *R. finalis* (7.1-86), *R. fossulatus* (7.1-85), *R. minutus* (7.1-86), *Retistephanocolporites festivus* (7.1-85, 86), *R. fossulatus* (7.1-85), *Retistephanoporites angelicus* (7.1-85–87), *R. crassiexinatus* (7.1-85), *R. minutiporus* (7.1-85), *Retisyncolporites angularis* (7.1-85, 86), *R. aureus* (7.1-86), *Retitrescolpites baculatus* (7.1-85), *R.* (?) *irregularis* (7.1-85), *R. magnus* (7.1-85), *R. peculiaris* (7.1-85), *R. saturum* (7.1-85), *Retitricolpites* (5.1-7), *R. absolutus* (7.1-86), *R. adeptus* (7.1-86), *R. adultus* (7.1-86), *R. americana* (7.1-66), *R. antonii* (7.1-86), *R. bonus* (7.1-86), *R. circumcanaliculatus* (7.1-96), *R. clarensis* (7.1-86), *R. conciliatus* (7.1-86), *R. constrictus* (7.1-86), *R. florentinus* (7.1-86), *R. incisus* (7.1-86), *R. lalongatus* (7.1-96), *R. magnus* (7.1-86, 91), *R. maledictus* (7.1-86, 87), *R. maturus* (7.1-86), *R. minutus* (7.1-86), *R. perditus* (7.1-86), *R. perforatus* (7.1-86), *R. retiaphelis* (7.1-96), *R. saturum* (7.1-86), *R. simplex* (7.1-86), *R. vetteri* (7.1-87), *Retitricolporites* (7.1-59, 64), *R. amazonensis* (7.1-66), *R. craceus* (7.1-86), *R. elegans* (7.1-96), *R. equatorialis* (7.1-86), *R. finitus* (7.1-86), *R. guianensis* (7.1-96), *R. hispidus* (7.1-86, 94, 96), *R. irregularis* (7.1-86, 87, 91), *R. magnus* (7.1-96), *R. marianis* (7.1-86), *R. mariposus* (7.1-94), *R. medius* (7.1-86, 87), *R. profundus* (7.1-86), *R. saskiae* (7.1-86), *Retitricolporoides* (5.1-7), *Retitriporites amplireticulatus* (7.1-85), *R. dubiosus* (7.1-86), *R. federicii* (7.1-86), *R. poricostatus* (7.1-85), *R. tilburgii* (7.1-86), *R. typicus* (7.1-86), *Rhamniphyllum casearifformis* (7.1-98), *Rhamnus fortinervosus* (7.1-15), *R. sanctaeflaviaensis* (7.1-15), R. sp. (7.1-15), *Rheedia* cf. *preacuminata* (7.1-15), *Rhizophora* (6.1-2; 7.1-96), *Rhoipites* (7.1-46), *R. cienagensis* (7.1-85), *R. guianensis* (7.1-85), *R. hispidus* (7.1-85), *R. squarrosus* (7.1-85), *Rhoophyllum serratum* (7.1-38), *Rhus* (7.1-57), *Rondeletia longiflorifolia* (7.1-41), *Rousea florentina* (7.1-85), *Rubicites chomeliifolia* (7.1-41), *Rugo[u]tricolporites felix* (7.1-85, 86), *Ruprechtia latipedunculata* (7.1-48), *Sabal ochseniusi* (7.1-58), *Sabicea* (?) *elliptica* (7.1-58), *Saccoglottis cipaconensis* (7.1-69, 70, 77), *Salacia floribundifolia* (7.1-15, 41), Sapindaceae type (7.1-61), *Sapindoides peruvianus* (7.1-69, 70, 72), *Sapindus acuminatus* (7.1-58), *S. argentinus* (7.1-41), Sapotaceae (7.1-96), *Sapotaceoidaepollenites* (4.1-10), *Scabraperiporites nativensis* (7.1-66), *Scabrastephanocolpites* (7.1-85), *Scabratricolpites simpliformis* (7.1-96), *S. tibialis* (7.1-86), *Scabratriporites moderatus* (7.1-86), *S. redundans* (7.1-86), *Schinopsis* (7.1-57), *S. balansiformis* (7.1-41), *S. morongifolia* (7.1-41), *S. patagonica* (7.1-15), *Schinus molliformis* (7.1-41), *Schizolobium inaequilaterum* (7.1-98), *Semitectotriporites gratus* (7.1-86), cf. *Senna* (7.1-57), *Serjania* (6.1-2), *S. itaquaquecetubensis* (7.1-98), *S. lancifolia* (7.1-98), *Siltaria mariposa* (7.1-85), *S. media* (7.1-85), *Simaruba versicoloroides* (7.1-77), *Spinozonocolpites* (7.1-91), *S.* aff. *baculatus* (7.1-85), *S. breviechinatus* (7.1-85), *S. echinatus* (7.1-66), *S. grandis* (7.1-85), *S. pachyexinatus* (7.1-85), *S. prominatus* (4.1-9), *Spirosyncolpites clavatus* (7.1-86), *S.*

spiralis (7.1-85–87), ?*Stenolobium rhomboidalis* (7.1-15), *Sterculia guinazui* (7.1-15, 41), *S. patagonica* (7.1-41), *S. washburnii* (7.1-15, 41), *Striacolporites pimulus* (7.1-96), *Striatopollis catatumbus* (7.1-85), *S. minor* (7.1-85), *S.* (?) *tenuistriatus* (7.1-85), *Striatricolpites cataumbus* (5.1-7; 7.1-86, 87), *S. gamerroi* (7.1-45), *S. minor* (7.1-96), *S. saramacensis* (7.1-96), *S. semistriatus* (7.1-86), *Striatricolporites angustinus* (7.1-86), *S. digitatus* (7.1-85), *Strychnos patagonica* (7.1-41), *Styloceras tertiarium* (7.1-41), *Styrax acuminatiformis* (7.1-41), *S. coriacea* (7.1-15, 58), *S. glabratoides* (7.1-15, 58), *S. glandulifera* (7.1-15, 41), *Symplocoipollenites* (4.1-10), *Symplocos commutatifolia* (7.1-41), *Syncolporites lisamae* (7.1-85), *S. marginatus* (7.1-85), *Tabebuia ipiformis* (7.1-15, 41), *Tecoma* (7.1-57), *T. serrata* (7.1-15, 58), *Terminalia* cf. *phaeocarpoides* (7.1-88), *Tetracera belensis* (7.1-70), *T. elliptica* (7.1-58), *T. patagonica* (7.1-41), *T. rhamnoides* (7.1-15, 58), *Tetracolporites pachyexinatus* (7.1-85), *T. psilatus* (7.1-85), *Tetracolporopollenites maculosus* (7.1-85), *T. spongiosus* (7.1-85), *T. transversalis* (7.1-85), *Tetragastris* (6.1-2), *Tetraplandra longifolia* (7.1-58), *Tetrapterys precrebrifolia* (7.1-15, 41), *Thevetia angustifolia* (7.1-58), *Thouinia philippii* (7.1-58), *Ticorea foetidoides* (7.1-58), *Tiliapollenites danei* (4.1-11), *T. vescipites* (4.1-10), cf. *Tillandsia* (6.1-2), cf. *Tontelea* (6.1-2), *Triatriopollenites guianensis* (7.1-96), *T. infernalis* (7.1-96), *T. lateflexus* (7.1-45), *Trichilia catignoides* (7.1-41), *T. moritziformis* (7.1-41), *Tricolpites* (7.1-59, 61, 64), *T. anguloluminosus* (7.1-44), *T. antonii* (7.1-85), *T. clarensis* (7.1-85), *T. gillii* (7.1-45), *T. incisus* (7.1-44), *T. protoclarensis* (7.1-85), *T. reticulatus* (7.1-44–46), *T.* cf. *variofoveatus* (4.1-10), *Tricolporites* (7.1-59), *T. microreticulatus* (7.1-61), *Tricolporopollenites hians* (7.1-66), *Triorites minor* (7.1-46), *Triporopollenites* (4.1-10; 5.1-7), *T.* (?) *tenuiexinatus* (7.1-85), *Triumfetta irregulariter-serrata* (7.1-15, 41, 58), *T. miocenica* (7.1-58), *Ulminium atlanticum* (7.1-39), *Ulmoideipites krempii* (7.1-66, 85), *Uragoga tertiaria* (7.1-70), *Vantanea columbiana* (7.1-75), *V. compressiformis* (7.1-70), *V. sheppardi* (7.1-72), *Venezuelites* (?) *distinctus* (7.1-85), *Verrustephanocolpites rugulatus* (7.1-85), *Verrustephanoporites* (7.1-85), *Verrutricolpites* (7.1-85), *V. irregularis* (7.1-86), *V. unicus* (7.1-86), *V. verrubolus* (7.1-96), *Verrutricolporites haplites* (7.1-86), *V. reticulatus* (7.1-85), *V. rotundiporus* (7.1-96), *Verrutriporites* (7.1-66), *Villaresia congonhifolia* (7.1-41), *Virola tertiaria* (7.1-70), *Vochysia dura* (7.1-58), *Wilsonipites margocolpatus* (7.1-85), *Zanthoxylon glanduliferum* (7.1-98), *Z. inaequabile* (7.1-58), *Z. tenuifolium* (7.1-58), *Zizyphus* (7.1-15, 57), *Zonocostites* (4.1-11), *Z. minor* (7.1-85), *Z. ramonae* (7.1-66). Incertae sedis: *Basopollis kurtz(s)chi* (5.1-6), *Carpolites cycaeformis* (7.1-58), *C. guilielmaeoides* (7.1-58), *Carpolithus belenensis* (7.1-69, 70), *C. bravoi* (7.1-69), *C. cissiformis* (7.1-70), *C. dicellaformis* (7.1-70), *C. inusitatus* (7.1-70), *C. jatrophaformis* (7.1-71), *C. olssoni* (7.1-69, 70), *C. patagonicus* (7.1-41), *C. peruvianus* (7.1-70), *C. pichileufensis* (7.1-41), *C. rutoides* (7.1-69, 70), *Classites capucinii* (7.1-86), *Clavainaperturites cordatus* (7.1-86), *Echinoidites problematicus* (7.1-86), cf. *Ephedripites* (7.1-86), *Peltandripites* (7.1-91), *Phyllites* (7.1-40, 41, 57), *P. acutoserratus* (7.1-58), *P. alsodeiaeoides* (7.1-58), *P. aspidospermaeoides* (7.1-58), *P. banisteriaeoides* (7.1-58), *P. coccolobaefolia* (7.1-58), *P. repandus* (7.1-58), *P. sauraujaeoides* (7.1-58), *P. ternstroemiaeoides* (7.1-58), *P. triplarioides* (7.1-58), *Retipollenites confusus* (7.1-86).

Oligocene, Oligo–Miocene, Miocene Amber
(*Hymenaea* spectrum)

[Note: Ref. 22 includes Holocene (zone 1), Quaternary (zone 2), late Pliocene (zone 3), and early Pliocene (zone 4); Mint Canyon (25) is probably Miocene]

Bacteria

Bacillus (5.1-19).

Fungi

Coprinites dominicana (5.1-11), *Entomophthora* (5.1-12), *Geastrum tepexensis* (4.1-12), *Geotrichites glaesarius* (5.1-13).

Algae and allied groups

Botrycoccus braunii (7.1-49, 52), *Chara woodringi* (5.1-16), *Chondrites dictyotoides* (5.1-8), *Pediastrum* (7.1-49, 52), *P.* cf. *duplex* (7.1-50), *Tasmanites* (7.1-52), zygospores of Zygnemataceae (7.1-49).

Bryophyta

Anthoceros (4.1-18), *Cinguitriletes australis* (7.1-49, 51, 52), *Sphagnum* (4.1-18).

Ferns and allied groups

Acrostichum mexicanum (4.1-24), *Alsophila* (5.1-20), *Anemia* (4.1-23), cf. *Antrophyum* (5.1-20), *Azolla* (7.1-52), *Baculatisporites* (7.1-49), *B. turbioensis* (7.1-51, 52), *Biretisporites* (4.1-11), *B. crassilabratus* (7.1-51, 52), *Ceratopteris* (4.1-21), *Cicatricosisporites* (4.1-11), *Cingutriletes australis* (7.1-49), *Cnemidaria–Hemitelia* (4.1-23; 5.1-10; see also *Hemitelia*), *Cyathea* (4.1-23; 5.1-10), Cyatheaceae (4.1-18), *Cyatheacidites annulatus* (7.1-49, 51, 52), *Cyathidites minor* (7.1-49, 52), *C. paleospora* (7.1-51, 52), *C. patagonicus* (7.1-52), *Deltoidospora* (7.1-51, 52), *D. minor* (4.1-11), *Densoisporites* (7.1-52), *Divisisporites* (7.1-50), *Echinatisporites* (4.1-11, 22), *E.* cf. *bockwitzensis* (4.1-22), *Equisetum* (7.1-62), *Faveasporis areapunctatis* (7.1-52), *F. palaequetrus* (7.1-52), fern spores (4.1-22), *Foveotriletes palaequetrus* (7.1-49, 52), *Gleichenia pectinataforma* (5.1-17), *Gleicheni(i)dites* (7.1-49), *G. circinidites* (7.1-52), *Grammitis succinea* (5.1-14), *Gymnogramme(a)* (*Hemionitis*) *wadii* (4.1-24), *G. woodringi* (5.1-16), *Hemitelia* (4.1-23), *H. brannerii* (5.1-8), *Ischyosporites areapunctatis* (7.1-49, 51, 52), Isoetaceae (4.1-18), *Isoetes* (?) *incerta* (5.1-8), *Jamesonia–Eriosorus* (5.1-10), *Laevigatosporites* (4.1-11, 18), *L. ovatus* (7.1-49, 51, 52), *Leiotriletes* cf. *regularis* (7.1-52), *Lepidosorus* (4.1-22), *Lycopodium* (4.1-18, 23; 5.1-10), *Lycopodiumsporites austroclavatidites* (7.1-51, 52), *Matonisporites ornamentalis* (7.1-49, 51, 52), monolete fern spores (*Laevigatosporites*, 5.1-20; *Verrucatosporites*; 4.1-21; 5.1-10), *Monolites alveolatus* (7.1-49), *Muricingulisporis chenquensis* (7.1-51, 52), *Peromonolites radiatus* (7.1-49), *P. vellosus* (7.1-49, 51, 52), Polypodiaceae (4.1-18), *Polypodiidites inangahuensis* (7.1-50), *Polypodiisporites* (4.1-22), *P.* cf. *alienus* (4.1-11), *P.* cf. *favus* (4.1-11, 22), *P. inangahuensis* (7.1-51, 52), *P.* cf. *megafavus* (4.1-11), *P.* cf. *minimus* (7.1-52), *P. radiatus* (7.1-51, 52), *P.* cf. *tenellis* (4.1-11), *P. undulatus* (4.1-22), *Polypodium* (4.1-23), *Pteris* (4.1-21, 23; 5.1-10, 20), *Regulatisporites mallatus* (7.1-52), *Reticuloidosporites tenellis* (7.1-51, 52), *Retitriletes austroclavatidites* (7.1-49), *Rouseisporites*

(7.1-49), *Selaginella* (4.1-21, 23; 5.1-10), Selaginellaceae (4.1-18), *Sphaeropteris–Trichipteris* (4.1-21), *Todisporites* (7.1-52), *T. major* (7.1-50), *Triletes*/trilete fern spores (4.1-22; 5.1-10, 20; 7.1-63), *Triletes paravallatus* (7.1-52), *Undulatisporites undulapolis* (4.1-22), *Verrucosisporites kopukeunsis* (7.1-52), Vittariaceae (cf. *Antrophyum*; 4.1-21).

Gymnosperms

Abies (4.1-18), *Abietineaepollenites* (4.1-11), *Araucaria nathorsti* (7.1-15), *Araucariacites australis* (7.1-49, 51, 52), *Assamiapollenites incognitus* (7.1-49), *Carollina torosus* (4.1-11), *Cedripites* (4.1-11), *Cupressus–Juniperus–Taxodium* (4.1-18), *Cycadaceae* (4.1-23), *Cycadopites* (4.1-11), *Dacri[y]dium* (4.1-18), *Dacrycarpites australiensis* (7.1-52), *Dacrydiumites florinii* (7.1-50), *Ephedra* (4.1-18), *Ephedripites multipartitus* (7.1-50), *Equisetosporites* (4.1-11), *E. claricristatus* (7.1-49, 51, 52), *E. lusaticus* (7.1-52), *E. notensis* (7.1-49, 52), *Gamerroites* cf. *psilasaccus* (7.1-49, 51, 52), *Ginkgo*? (7.1-15), *Inaperturopollenites hiatus* (7.1-52), *Lygistepollenites florinii* (7.1-49, 51, 52), *Microcachryidites antarcticus* (7.1-49–52), *Phyllocladidites mawsonii* (7.1-49, 51, 52), *P.* cf. *verrucosus* (7.1-51), *Picea* (4.1-18, 21), *Pinus* (4.1-18, 20, 22, 23; 5.1-9, 20), *Podocarpidites* (7.1-63), *P. elegans* (7.1-49, 51, 52), *P.* cf. *ellipticus* (7.1-49, 52), *P.* cf. *exiguus* (7.1-52), *P. marwickii* (7.1-49–52), *P. rugulosus* (7.1-49, 52), *P.* cf. *verrucosus* (7.1-50), *Podocarpus* (4.1-18, 20; 5.1-10; 7.1-94), *Pristinuspollenites* (4.1-11), *Protodiploxypinus* (7.1-50), *Trisaccites microsaccatum* (7.1-49, 51, 52), *Zamia collazoensis* (5.1-8), *Z. noblei* (5.1-8).

Angiosperms

Abutilon (5.1-10), *Acacia* (4.1-18, 19, 25; 5.1-10), *A. eocaribbeanensis* (5.1-18), *Acaciapollenites myriosporites* (7.1-52), *Acalypha* (4.1-25), Acanthaceae (4.1-18), *Acrodiclidium pseudocanelo* (5.1-8), *A. pseudosalicifolium* (5.1-8), *Aesculus* (4.1-25), *Aetanthus* (5.1-10), Agavaceae (4.1-18), *Ailanthipites* cf. *marginatus* (7.1-50), *Alchornea* (5.1-10, 20), *Alfaroa–Oreomunnea* (4.1-21; 5.1-20), *Allamanda carmensis* (4.1-24), *Allophylus* (5.1-20), *Ambrosia* type (4.1-22), Anacardiaceae (4.1-18; 7.1-94), *Anacardioxylon caracoli* (7.1-78c; 7.2-35), *Anacardites lanceolatus* (4.1-24), *Aniba collazoensis* (5.1-8), *Annona cetera* (5.1-8), *A. pseudoglabra* (5.1-8), *A. saraviana* (4.1-24), *Apocynophyllum mexicanum* (4.1-24), *A. pseudowillughbya* (5.1-8), *A. wilcoxense* (?) (5.1-8), Araliaceae (7.1-94), *Arctostaphylos* (4.1-25), *Arecipites* (4.1-11), *A.* cf. *multiscabratus* (7.1-51), *A. subverrucatus* (7.1-49, 52), *Armeria* (4.1-18), *Artemisia* type (4.1-22), *Aspidosperma collazoensis* (5.1-8), *Ayenia* (4.1-23), *Baccharis* (4.1-25), *Bactris pseudocuesco* (5.1-8), *Baumannipollis variaperturatus* (7.1-49, 51, 52), *Bernoullia* (5.1-10), *Betula* (4.1-18), *Bignonia zulliana* (5.1-17), Bignoniaceae (4.1-18), *Bignonoides orbicularis* (4.1-24), Bombacaceae (cf. *Aguiaria* type; 4.1-21), *Bombacacidites* (4.1-18), *Bombax* (4.1-22; 5.1-10), Boraginaceae (4.1-18), *Brahea* (4.1-25), *Bredeliapollis* (7.1-51), *Brickellia* (4.1-25), *Brunellia* (5.1-10), *Bucida sanchezensis* (5.1-15), *Bumelia cunaetafolia* (5.1-16), *B. reclinatafolia* (5.1-15), *B. retusafolia* (5.1-17), *Bursera* (4.1-18, 25; 5.1-10), *Caesalpinia* (4.1-25), *C. prebahamensis* (5.1-17), *Caesalpinites incertus* (5.1-17), *Calophyllum calabaformis* (5.1-17), *Calyptranthes domingensis* (5.1-15), *Canthiumidites* aff. *bellus* (7.1-51, 52), *Capparis prejamaicensis* (5.1-17), *Cardiospermum* (4.1-25), *Carya* (4.1-18, 23), *C.* type [?] (7.1-63), Caryophyllaceae (4.1-18), *Casearia* (5.1-10), *Cassia* (4.1-25), *C.* (?) *dubiosa* (5.1-8), *C. evidens* (5.1-8), *C. imitativa* (5.1-8), *C. imparilis* (5.1-8), *C. ordinaria* (5.1-8), *C. puryearensis* (5.1-8), *C. visibilis* (5.1-8), *C. yumuriensis* (5.1-17), *Castanea* (4.1-18), *Castaneapollenites* (4.1-11), *Catostemma* (5.1-10; *C.* type 7.1-94), *Ceanothus* (4.1-25), *Cedrela* (4.1-21), *C. miocenica* (4.1-24), *Cedrelospermum manchesteri* (4.1-13), *Celastrus simplex* (5.1-17), *Celtis* (4.1-25), *Cercocarpus* (4.1-25), *C. mixteca* (4.1-14), Chenopodiaceae–Amaranthaceae–chenoams (4.1-18; 5.1-20), *Chenopodipollis* (7.1-51), *C. chenopodiaceoides* (7.1-49, 52), *Chiococca* (4.1-25), *Chrysophyllum* (5.1-10), *C. cahobasensis* (5.1-16), *C. comparabile* (5.1-8), *C. pseudargenteum* (5.1-8), *C. pseudargenteum* var. *oblongum* (5.1-8), *Clavainaperturites clavatus* (7.1-94), *Clavatipollenites* (7.1-49, 51, 52), Clethraceae (4.1-18), *Colubrina* (4.1-25), *Comarostaphylis* (4.1-25), *Combretum pseudojacquinii* (5.1-8), *Comocladia intermedia* (4.1-17), Compositae (4.1-18; 5.1-20), Compositae type [?] (7.1-63), *Compositoipollenites* aff. *tarragoensis* (7.1-51), *Condalia* (4.1-25), *Connarus carmenensis* (4.1-24), *Copaiva oligocenica* (5.1-8), *Corsinipollenites* (4.1-18), *C. atlantica* (7.1-49, 52), *Corylus* (4.1-18), *Corynostylis* (5.1-10), *Coussapoa veracruziana* (4.1-24), *Crescentia cucurbitinoides* (4.1-24), *Crossosoma* (4.1-25), *Crudia* (4.1-21), cf. *Cryosophila* (4.1-21), *Cupanieidites reticularis* (7.1-49, 51, 52), *Cynometra rabellii* (5.1-8), Cyperaceae (4.1-22), *Cyperaceapollis neogenicus* (7.1-49, 52), *Dalbergia hesperia* (5.1-17), *Dalea* (4.1-25), *Dendropanax* (5.1-10), *Dichromena* (4.1-25), *Dioclea* (?) *mexicana* (4.1-24), *Diospyros* (4.1-25), *Dipholis pseudoleiantha* (5.1-8), *Diporites* (7.1-49), *D. aspis* (7.1-51, 52), *Dodonaea* (4.1-25), *D. cubensis* (5.1-17), *Dorstenia* (4.1-18), *Drosera* (4.1-18), *Dryadopollis minima* (7.1-52), *Drypetes elliptica* (4.1-24), *D. laterifloraforma* (5.1-17), *Echimonocolpites franciscoi* (7.1-94), *Echiperiporites* (4.1-11), (*Echi-*?)*periporites akanthos* (7.1-94), *Echites pseudostellaris* (5.1-8), *Engelhardia* (4.1-20, 23; 5.1-10), *Eperua* (4.1-23), Ericaceae (4.1-21), *Ericipites* (7.1-49, 52), *Eucommia* (4.1-18), *Eucommia constans* (4.1-15), *Eugenia–Myrcia* (4.1-21; 5.1-10), *Eugenia comparabilis* (5.1-8), *E. ovatifolia* (5.1-17), *E. pseudaeruginea* (5.1-8), *Euphorbia* (4.1-18, 25), *Exostema precaribaeum* (5.1-17), *Eysenhardtia* (4.1-25), *Fagara miocenica* (5.1-17), *F. wadii* (4.1-24), *Fagus* [?] (5.1-10) *F.* [?, *Nothofagus*] *morenoi* (7.1-15), *F. obscura* (7.1-15), *Faramea* (5.1-10), *Fendlera* (4.1-25), *Ficus hyphodroma* (5.1-8), *F. schimperii* (5.1-8), *F. talamancana* (4.1-24), *F. vexativus* (5.1-8), *Forestiera* (4.1-25), *Fouquieria* (4.1-25), *Fraxinus* (4.1-25), *Fremontodendron* (4.1-25), Gesneriaceae (4.1-18), *Glenopollis ornatus* (7.1-52), *Goeppertia* cf. *tertiaria* (4.1-24), *Gouania miocenica* (4.1-24), *Goupioxylon stutzeri* (7.2-35), Gramineae (4.1-18, 22, 23; *Monoporites*), *Graminidites* (4.1-11; 7.1-49, 51, 52), *Guarea* (4.1-21; 5.1-10), *G. opinabilis* (5.1-8), *Guettarda cookei* (4.1-24; 5.1-15, 16), *G. intercalaris* (5.1-8), *Guttiferoxylon compactum* (7.1-78c; 7.2-35), *G. platonioides* (7.2-35), *Haloragacidites trioratus* (7.1-52), *Hancornia minor* (5.1-8), *H. pseudopubescens* (5.1-8), *Haplorhus medranoensis* (4.1-17), *Hauya* (5.1-10), *Hedyosmum* (4.1-22), *Helianthus* type (4.1-22), *Heliconia* (5.1-17), *Heliocarpus* (4.1-18), *Holodiscus* (4.1-25), *Hufelandia portoricensis* (5.1-8), *Hygrophila* (5.1-20; also under Oligo–Miocene), *Icacorea* sp. (?) (7.1-8), *I. prisca* (5.1-8), *Ilex* (4.1-18, 23,

25; 5.1-10; 7.1-94), *Inga curta* (5.1-8), *I. leonii* (5.1-17), *I. miocenica* (4.1-24; 5.1-17), *I. pseudinsignis* (5.1-8), *I. pseudonobilis* (5.1-8), *I. pseudospuria* (5.1-8), *I. sanchezensis* (5.1-15), *Intratriporopollenites* (7.1-52), *Iriartea collazoensis* (5.1-8), *Iriartites vaughani* (6.1-3), *Jacaranda* (5.1-10), *Juglans* (4.1-18, 25), *Jussitriporites* cf. *undulatus* (4.1-22), *Karwinskia axamilpense* (4.1-16), Labiatae (4.1-18), *Laguncularia racemosafolia* (5.1-17), *Laurocerasus* (4.1-25), *Lecythidophyllum bolivarensis* (7.1-78b), *L. couratarioides* (4.1-24), Leguminosae (4.1-18), Leguminosae–Caesalpiniaceae (4.1-18), *Leguminosites mexicanus* (4.1-24), *L. oaxacensis* (4.1-24), *Leguminoxylon grossei* (7.1-78c; 7.2-35), Liliaceae (4.1-18), *Liliacidites* (4.1-23; 7.1-49, 52), *L. variegatus* (4.1-11; 7.1-51), *Lippia* (4.1-25), *Liquidambar* (4.1-18; 5.1-10[?]), *L. incerta* (4.1-24), *Lonchocarpus praelatifolius* (5.1-8), *Lyonothamnus* (4.1-25), *Lysiloma* (4.1-25), *Magdalenophyllum aequilaterum* (4.1-13), *Mahonia* (4.1-25), Malpighiaceae (4.1-18; 5.1-20; 7.1-94), Malvaceae (7.1-94), *Malvacipolloides comodorensis* (7.1-52), *Malvocarpon clarum* (5.1-8), *Manicaria portoricensis* (5.1-8), *Marcgravia* (5.1-10), *Margocolporites* (7.1-50), *M. tenuireticulatus* (7.1-49, 51, 52), *M. vanwijhei* (7.1-52), Melastomataceae (7.1-94), *Melastomites angustus* (4.1-24), *M. domingensis* (5.1-15), *M. obovatus* (4.1-24), Meliaceae (4.1-18), *Melicoccus immutata* (5.1-8), *Mespilodaphne hispaniolana* (5.1-16), *M. palomaresensis* (4.1-24), *Metopium prenuntium* (5.1-17), *Milfordia argentina* (7.1-52), *Mimusops leonii* (5.1-17), *M. miocenica* (5.1-17), *M. praeparvifolia* (5.1-16), *Misanteca dubiosa* (5.1-8), *Momipites anellus* (4.1-11), *M. corylipites* (4.1-11), *M. coryloides* (4.1-18), *M. microcoryphaceous* (4.1-18), *M. microfoveolatus* (4.1-11), *M. triorbicularis* (4.1-18), *M. triradiatus* (4.1-18), *Monocolpites medius* (7.1-94), *Moquilea mexicana* (4.1-24), Moraceae (4.1-18), *Multiaerolites formosus* (4.1-22), *Multisiapollis viteauensis* (7.1-49), *Musophyllum* (5.1-8), *Mutisiapollis viteauensis* (7.1-52), *Myrcia* (as *Myrica*; 5.1-10), *M. denuntiativa* (5.1-8), *M. eugenioides* (5.1-8), *M. minor* (5.1-17), *M. prerostrata* (5.1-17), *M. saraviana* (4.1-24), *Myrsine pseudoferruginea* (5.1-8), Myrtaceae (4.1-18; 7.1-94), *Myrtaceidites* (7.1-50, 63), *M. verrucosus* (7.1-49, 51, 52), *Myrtiphyllum bagualense* (7.1-15), *Nectandra areolata* (4.1-24), *N. tehuantepecensis* (4.1-24), *Norantea* (4.1-23; 5.1-10), *Nothofagidites* (7.1-63), *N. acromegacanthus* (7.1-49, 51, 52), *N. americanus* (7.1-49, 51, 52), *N. dorotensis* (7.1-49, 51, 52), *N. flemingii* (7.1-49, 51, 52), *N. incrassatus* (7.1-50), *N. micromarginatus* (7.1-50), *N. saraensis* (7.1-49–52), *N. tehuelchesii* (7.1-49, 51, 52), *N. visserensis* (7.1-50), *Nothofagus* (4.1-11; see also *Fagus*), *N. crenulata* (7.1-15), *N.* cf. *densinervosa* (7.1-62), *N. elongata* (7.1-15), *N. lanceolata* (7.1-15), *N. serrulata* (7.1-15), *Nyssa* (5.1-10, ?), *N. variabilis* forma *oblonga* (7.1-15), *Nyssapollenites endobalteus* (7.1-51, 52), *Oreodaphne mississippiensis* (5.1-8), *Oryctanthus* (5.1-20), *Oxalis* (5.1-10), *Pachira* (4.1-20), *Pachycormus* (4.1-25), *Pachydermites diederixi* (4.1-22), palm rays (4.1-24; 5.1-17), *Palmacites alius* (5.1-8), *P. conformis* (5.1-8), *P. sparsistriatus* (5.1-8), Palmae (4.1-18, 21; 5.1-20), *Palmocarpon acrocomioides* (5.1-8), *P. cetera* (5.1-8), *P. exemplare* (5.1-8), *P. genomoides* (6.1-4), *P. opinabile* (5.1-8), *P. rabellii* (5.1-8), *Palmophyllum* (5.1-8), *Pandanus* (4.1-18), *Parsonsidites conspicuos* (4.1-11), *Passiflora* (4.1-25), *Pelliceria* (4.1-20, 21, 23; 5.1-10), *Pellicieroipollis* (4.1-11), *Persea* (4.1-25), *Piscidia* (4.1-25), *Pisonia conditi* (5.1-15, 16), *P. longifoliaformis* (5.1-17), *Pistacia* (4.1-25), *P. marquezii* (4.1-17), *Pithecellobium* (4.1-25), *P.* (?) *imperfectum* (5.1-8), *P. pseudotrapezifolium* (5.1-8), *P. samanensis* (5.1-15), *P. vexativum* (5.1-8), *P. yumuriensis* (5.1-17), *Platanus* (4.1-18, 25), *Pleodendron* (5.1-10), *Plumiera evidens* (5.1-8), *Poacites* (5.1-15), *Poluspissusites* (7.1-49, 51), *P. puntensis* (7.1-52), *Polyadopollenites* (7.1-52), Polygalaceae (4.1-18), Polygonaceae (4.1-18), *Polyporina romeroi* (7.1-50), Pontederiaceae (4.1-18), *Populus* (4.1-25), Portulacaceae (4.1-18), *Potamogetonaceapites* (7.1-50), Proteaceae type (7.1-63), *Proteacidites obscurus* (7.1-51, 52), *P. pseudomoides* (7.1-49, 52), *Proxapertites* (4.1-22), *Prunus* (4.1-25), *Pseudolmedia spuriaformis* (5.1-17), *Pseudosmodingium mirandae* (4.1-Ramírez et al., 2000), *P. terrazasiae* (4.1-Ramírez et al., 2000), *Pseudowinterapollis couperi* (7.1-49, 51, 52), *Psidium dissimile* (5.1-8), *Psiladiporites minimus* (7.1-94), *Psilamonocolpites medius* (7.1-94), *Psilatricolpites psilascabratus* (7.1-50), *Psilatricolporites* (7.1-50), *P. crassus* (4.1-11; 7.1-94), *P. operculatus* (7.1-49, 52, 94), *P. rotundiporus* (7.1-94), *P. triangularis* (7.1-94), *Pterocarya* (4.1-18), *Quercus* (4.1-18, 22, 25), *Quintinaipollis striatulosa* (7.1-52), *Rau(v)wolfia* (5.1-10), *Reevesia* (4.1-18), *Retistephanocolporites quadriporus* (7.1-94), *Retitricolporites cienaguensis* (7.1-52), *R. guianensis* (7.1-94), *R. hispidus* (7.1-94), *R. irregularis* (7.1-94), *R. squarrosus* (7.1-94), *Reynosia latifolioides* (5.1-17), *Rhabdadenia* (4.1-18), *Rhamnus* (4.1-25), *Rheedia silvargillacea* (5.1-17), *Rhizophora* (4.1-20, 21, 23; 5.1-10; 7.1-94), *R.* (?) *doctrinalis* (5.1-8), *Rhoipites baculatus* (7.1-49–52), *R. cienaguensis* (7.1-49, 52), *R. romeroi* (7.1-52), *Rhoophyllum serratum* (7.1-15), *Rhus* (4.1-17, 25), *R. toxicodendroides* (4.1-17), *Robinia* (4.1-25), *Rondeletia* (?) (4.1-24), Rosaceae (4.1-18), *Rubipollis oblatus* (7.1-52), Rutaceae (4.1-18), *Sagittaria* (4.1-18), *Salix* (4.1-25; 5.1-10), Sapindaceae (4.1-18), *Sapindus* (4.1-25), *Sapindoxylon antioquiense* (7.1-78c; 7.2-35), *S. brittonii* (5.1-8), *S. gracilentus* (5.1-8), *S. hispaniolana* (5.1-15), *S. obesus* (5.1-8), *S. presaponaria* (5.1-17), *S. pseudomarginatus* (5.1-8), *Sapota agnitionalis* (5.1-8), Sapotaceae (4.1-18, 22; 7.1-94), *Schaefferia* (4.1-25), Scrophulariaceae (4.1-18), *Senipites patagonica* (7.1-51, 52), *Sideroxylon aequale* (5.1-8), *Simaruba glaucaformis* (5.1-17), *S. haitensis* (5.1-16), *S. veracruziana* (4.1-24), *Smilacipites saltensis* (7.1-50), *Socratea brownii* (4.1-Poinar, 2002), Solanaceae (4.1-18), *Sophora cookei* (5.1-15), *S. maranoides* (5.1-17), *S. matanzana* (5.1-17), *S.* (?) *suspecta* (5.1-8), *S. yumuriensis* (5.1-17), *Sparcipollis* (7.1-49, 51), *Sparganiaceaepollenites barungensis* (7.1-49–52), *Spinitricolpites* (7.1-51), *Striasyncolpites laxus* (7.1-49, 52), *Striatricolporites gamerroi* (7.1-49, 51, 52), *Stylogyne* (?) *fragmenta* (5.1-8), *Swietenia mahagoniformis* (5.1-17), *Tapirira* (4.1-25), *T. durhamii* (4.1-19), *Tecoma* (5.1-10), *Terminalioxylon naranjo* (7.1-78c; 7.2-35), *T. porosum* (7.2-35), *Tetrorchidium* (5.1-10), *Thouinia* (4.1-25), Tiliaceae (4.1-18), *Tiliapollenites danei* (4.1-11), *Tillandsia* (4.1-23), *Tournefortia* (5.1-10), *Trichilia evidens* (5.1-8), *T. hirtaformis* (5.1-17), *T. pseudobakerii* (5.1-8), *T. pseudohirta* (5.1-8), *T. spatulata* (5.1-8), *Tricolpites asperamarginis* (7.1-51), *T. reticulatus* (7.1-49–52), *T. trioblatus* (7.1-49, 52), *Triorites minor* (7.1-52), *Triporopollenites* (7.1-49), *Trithrinax dominicana* (5.1-14), *Tubulifloridites* (7.1-51), *T. antipodica* (7.1-52), *T. viteauensis* (7.1-52), *Typha* (4.1-18, 25), Ulmaceae (4.1-18), Urticaceae (4.1-18), *Verrutricolporites rotundiporus* (7.1-94), *Vitis* (4.1-25), *Zanthoxylum* (5.1-10), *Zizyphus elliptica* (5.1-17), *Z. minor* (5.1-17), *Z. pseudochloroxylon*

(5.1-8), *Zonocostites* (4.1-11). Incertae sedis: *Aglaoredia* (4.1-18), *Antholithus heimiaformis* (5.1-17), *Catinipollis* (4.1-18), *Concentricystis* (4.1-22), *Corsinipollenites* (4.1-18), *Cretacaeiporites* (4.1-18), *Echitonium* (?) (5.1-8), *Erdtmanipollis* (4.1-18), *Foraminisporis* cf. *foraminis* (4.1-22), *Malvacipollis* (4.1-18), *Nuxpollenites* (4.1-18), *Ramulus* (?) (5.1-8), *Rugubivesiculites* (4.1-18), *Triplanosporites* (4.1-22), *Trithrinax dominicana* (5.1-Poinar, 2002).

Miocene

Fungi

Ascomycete cleistothecium (6.1-9), *Circulisporites* (7.2-45), *Diporisporites* (7.2-45), *Lacrimasporonites* (7.2-45), *Tetraploa* cf. *aristata* (7.2-50).

Algae and allied groups

Botryococcus (7.2-10, 43, 50), *Chondrites subsimplex* (7.2-19a), *Mougeotia* (7.2-43), *Operculodinium centrocarpus* (6.1-9), *Pediastrum* (7.2-10, 43, 50), Pyrrophyta (6.1-10), *Spiniferites* (6.1-9).

Bryophyta

Baccania, *Drepanolejuenia*, *Frullania*, *Octoblepharum* (see Miocene amber), *Ricciaesporites* (7.2-10), *R. transdanubicus* (7.2-13).

Ferns and allied groups

Acrostichum (6.1-6), *A. linearifolium* (7.2-21), *Adiantides borgoniana* (7.2-19a), *Alsophila* (6.1-10), *Alsophilocaulis calveloi* (7.2-1), *Antrophyum* (6.1-7–9), *Asplenium* (7.2-16), *Azolla* (7.2-13, 43), *Bacutriletes* (7.2-50), *Biretisporites* (7.2-10), *Blechnum* (7.2-16), *B. antediluvianum* (7.2-19a), *B. betijoquensis* (7.2-40), *Ceratopteris* (6.1-8, 10), *Cicatricosisporites baculatus* (7.2-43), *C. dorogensis* (7.2-43), *Cingulatisporites* (7.2-43), *Clavatriletes* (7.2-50), *Cnemidaria* (6.1-10), *Crassoretitriletes vanraadshooveni* (7.2-43, 50), *Ctenitis* (6.1-10; 7.2-16), *Cyathea* (6.1-7–10), *Cyatheacidites* (7.2-50), *C. annulatus* (7.2-43), *Cyathidites* (7.2-45), *Danaea* (6.1-7), *Deltoidospora* (7.2-10), *D. adriennis* (7.2-43, 50), *Dictyophyllidites chiquimilense* (7.2-12), *Echinatisporites* (4.1-22), *Echinosporis* (7.2-43, 50), *Echinosporites* (4.1-22), *E.* cf. *E. bockwitzensis* (4.1-22), *Echitriletes muelleri* (7.2-43, 50), *Equisetites* (7.2-5), *Equisetum* (7.2-16), *Foveotriletes* cf. *labrus* (7.2-13), *F. margaritae* (7.2-43), *F. ornatus* (7.2-43, 50), *Grammitis* (6.1-10), *Gymnogramme(a)* (?) (7.2-21), *Intrapunctatisporites* (7.2-45), *Kuylisporites waterbolki* (7.2-43, 50), *Laevigatosporites catanejensis* (7.2-43, 50), *L. ovatus* (7.2-13), *L. vulgaris* (7.2-43), *Leiotriletes* (7.2-10), *Lepidosorus* (4.1-22), *Lomariopsis tertiaria* (7.2-21), cf. *Lophosoria* (7.2-16), *Lycopodium* (6.1-7, 9, 10), *Lygodium* (6.1-7), *Magnastriatites grandiosus* (7.2-43, 50), *Matonisporites* (7.2-45), *M. mulleri* (7.2-50), monolete fern spores (5.1-20; 6.1-7–10), *Muricingulisporis verrucosus* (7.2-12), *Nijssenosporites fossulatus* (7.2-43), *Ophioglossum* (6.1-10), *Osmundacidites* (7.2-45), *Pecopteris* (7.2-21; undeterminable fragment of Paleozoic fern-like foliage), *P. buhsei* (7.2-19a; undeterminable fragment of Paleozoic fern-like foliage), *Perinomonoletes* (7.2-43, 50), *Polypodiaceaesporites* (7.2-45), *Polypodiaceoisporites* (7.2-50), *P. pseudopsilatus* (7.2-43), *P.* cf. *speciosus* (7.2-43), *Polypodiisporites* (4.1-22), *P. favus* (4.1-22), *P. undulatus* (4.1-22), *Psilamonoletes tibui* (7.2-50), *Psilatriletes lobatus* (7.2-50), *P. peruanus* (7.2-50), *P.* sp. 1, 2 (7.2-50), *Pteris* (6.1-7–10), *P. cousiniona* (7.2-19a), *Retitriletes sommeri* (7.2-43), *Rugotriletes* (7.2-50), *Selaginella* (6.1-7–10), trilete fern spores (6.1-7–10), *Triletes* cf. *tuberculiformis* (7.2-13), *Undulatisporites undulapolis* (4.1-22), *Verrucatosporites* (7.2-45), *V.* cf. *speciosus* (7.2-43), *V. usmensis* (7.2-43, 50), *Verrucatotriletes* cf. *bullatus* (7.2-43, 50), *Verrutriletes* (7.2-50). Incertae sedis: *Filicites* (7.2-16).

Gymnosperms

Araucaria (7.2-16, 17), *Araucarioxylon chilense* (7.2-18), *Austrocedrus* (7.2-17), *Dacrydium* (7.2-17), *Ephedra* (7.2-19a), *Equisetosporites claricristatus* (7.2-10, 13), *E. fusiformis* (7.2-13), *E. lusaticus* (7.2-10, 13), *E. notensis* (7.2-10, 13), *Fitzroya tertiaria* (7.2-5), *Podocarpidites* (7.2-43, 45, 50), *P. elegans* (7.2-10), *P.* cf. *ellipticus* (7.2-10), *P. marwickii* (7.2-13), *P. rugulosus* (7.2-13), *Podocarpus* (6.1-10; 7.2-16, 17), *P. fossilis* (7.2-21), *Saxegothopsis* (7.2-16, 17), *Sequoia chilensis* [?] (7.2-19a), *Zamia tertiaria* (7.2-19a).

Angiosperms

Acacia (6.1-7, 10), *A. dimidiato-cordata* (7.2-21), *A. tenuifolia* (7.2-21, 23), *A. uninervifolia* (7.2-21), *Acaciapollenites myriosporites* (7.2-9, 13), *Acrodiclidium oligocaenicum* (7.2-19a), *Aegiphila* (6.1-10), *Aextoxicoxylon harambouri* (7.2-15), *Agonis* (7.2-16), cf. *Aguiaria* (6.1-9, 10), *Ailanthipites* cf. *marginatus* (7.2-13), *A.* cf. *nonprolatus* (7.2-13), *Alchornea* (6.1-7–10), *Alfaroa–Oreomunnea* (6.1-8–10), *Allamanda crassostipitata* (7.2-19a), *Allophylus* (6.1-7, 10), *Alnipollenites verus* (7.2-43), *Alnus* (7.2-14), *Amicia antiqua* (7.2-22), *Amomyrtus* (7.2-16), *Ampelodaphne grandifolia* (7.2-19a), *Anacardites americanus* (7.2-41, 44), *A. spondiaeformis* (7.2-44), *Anacolosidites* cf. *lutoides* (7.2-43), *An(n)ona coronelensis* (7.2-19a), *A. guppyi* (7.2-33, 40), *A. speciosa* (7.2-19a), *A. winslowiana* (7.2-28a), *Antholithus venezuelensis* (7.2-40), *Antidaphne lotensis* (7.2-19a), *Apocynophyllum chilense* (7.2-19a), *A. salvadorensis* (7.2-40), *Ardisia crassifolia* (7.2-19a), *Arecipites* (7.2-45), *Arrabidaea patagonica* (7.2-19b), *Arthante* [*Artanthe*] *geniculatoides* (7.2-19a), *Attalea* type (6.1-9), *Aulomyrcia* (7.2-16), *Avicennia miocenica* (7.2-33), *Bambusium stubeli* (7.2-28a), *Banara cuadrae* (7.2-19a), *B. prehernandiensis* (7.2-19b), *Banisteria bassleri* (7.2-28b), *B. incerta* (7.2-28a), *B. praenuntia* (6.1-6), *Baumannipollis chubutensis* (7.2-13), *B. variaperaturatus* (7.2-10), *Benettia grosse-serrata* (7.2-19a), *Berberis* (7.2-16), *Bernoulia* (6.1-10), *Bignonia gigantifolia* (7.2-19a), *B. neogenia* (7.2-28b), *Bignonites americanum* (7.2-28b), *B. chalianus* (7.2-5), *B. ovatus* (7.2-19b), *Bombacacidites araracuarensis* (7.2-50), *baculatus* (7.2-43, 50), *B. baumfalki* (7.2-43, 50), *B. bellus* (7.2-43, 50), *B. ciriloensis* (7.2-43), *B. muinaneorum* (7.2-50), *B. zuatensis* (7.2-43), *Bombacaciphyllum opacum* (7.2-19a), *Bombax* (4.1-22), *B. firmifolium* (7.2-19a), *B. playense* (7.2-19a), *B. prebarrigon* (7.2-44), *Boquila* (7.2-16), *Brosimum miocenicum* (7.2-44), cf. *Bucida* (6.1-10), *Bue(y)ttneria* (7.2-33), cf. *Bumelia* (6.1-10), *B. trinitense* (7.2-44), *Bursera* (6.1-10), *Burserites venezueleana* (7.2-40), *Cabomba* (6.1-10), *Caesalpinia gmehlingi* (7.2-21), *Caladiosperma miocenica* (7.2-41, 44), *Caldcluvia* (7.2-16), *Calliandra* (7.2-11), *C. obliqua* (7.2-21), *C. ovatifolia* (7.2-21), *Callistemon* (7.2-16), *Calophyllum calabaformis* (7.2-44), *Calyptranthes gatunensis* (6.1-6), *Camphoromoea*

speciosa (7.2-19a), *Canavalia miocenica* (7.2-44), *Capparis multinervis* (7.2-21), *Casearea* (6.1-7), *C. oliganthoides* (7.2-19a), *C. piparoides* (7.2-19a), *C. spinuloso-serrata* (7.2-19a), *Casimiroa* (6.1-10), *Cassia* (7.2-14), *C. aguaytiensis* (7.2-28b), *C. argentinensis* (7.2-14), *C. bassleri* (7.2-28b), *C. chrysocarp[i]oides* (7.2-20–22), *C. cristoides* (7.2-20, 22), *C. culebrensis* (6.1-6), *C. kugleri* (7.2-44), *C. leptocarpoides* (7.2-44), *C. ligustrinoides* (7.2-20–22), *C. longifolia* (7.2-44), *C. membranacea* (7.2-21), *C. obscura* (7.2-21), *C. rigidulifolia* (7.2-21, 23), *C. sipariensis* (7.2-44), *C. wendtii* (7.2-22), *C. zuliana* (7.2-44), *Casuarina patagonica* (7.2-3), *Cedrela* (6.1-10), *C. preodorata* (7.2-44), *C.* (?) *tertiaria* (7.2-44), *Ceiba* (6.1-9, 10), *Celtis ameghenoi* (7.2-19b), chenoams (6.1-7), *Chenopodipollis chenopodiaceoides* (7.2-10, 13), *Chomelia* type (6.1-10), cf. *Cionosicys* (6.1-10), *Cissus pichinleufuensis* (7.2-14), *Clavainaperturites clavatus* (7.2-43), *C. microclavatus* (7.2-50), *Clavamonocolpites* (7.2-50), *C. lorentei* (7.2-43), *Clavatricolporites* cf. *leticiae* (7.2-43), *Clusia vera* (7.2-44), *Colubrina miocenica* (7.2-41, 44), *Combretum incertum* (7.2-44), *C. oblongifolium* (7.2-19a), *Combretum–Terminalia* (6.1-7, 10), Compositae (6.1-7, 8; Mutisieae type, 6.1-10), *Compositoipollenites* (7.2-45), *Condaminea grandifolia* (7.2-28a), *Copaifera reticulata* (7.2-19a), *Cordia pulchra* (7.2-19a), *Corsinipollenites* cf. *exinitenuis* (7.2-13), *C. oculusnoctis* (7.2-43, 50), *Cosmibuena* (6.1-10), *Costus* (?) *incertus* (7.2-44), *Couroupita santanderensis* (7.2-33), *Coussapoa* (7.2-33), *C. quinquenervis* (7.2-19a), *C. vaningeni* (7.2-44), *C. villosoides* (7.2-40), *Coussarea membranacea* (7.2-19a), *Crassiectoapertites columbianus* (7.2-43, 50), *Cricotriporites guianensis* (7.2-13, 50), *Crototricolpites annemariae* (7.2-43, 50), *Crudia* (6.1-8–10), *Cryosophila* type (6.1-7, 8), *Cupania* (6.1-7, 10), *C. grosse-serrata* (7.2-19b), *C. inserta* (7.2-19b), *C. latifolioides* (7.2-19b), *Cuphea antiqua* (7.2-22), *Cupuliferoidaepollenites* (7.2-45), *Cymbopetalum* (6.1-10), *Cyperaceaepollis* (7.2-50), *C. neogenicus* (7.2-10, 13, 43), *Cyrillaceaepollenites* (7.2-45), *Dalbergia antiqua* (7.2-21), *D. chartacea* (7.2-21), *Desfontainia* (7.2-16), *Desmodium ellipticum* (7.2-21), *D. obliquum* (7.2-19a), *Desmoncus* type (6.1-7), *Dioscorea* (7.2-16, 33), cf. *Dioscorea–Rajania* (6.1-7), *Diospyros macdonaldi* (6.1-6), *Doliocarpus* (6.1-7), *D. oblongifolia* (7.2-19a), *D.* (?) *serrulata* (7.2-19a), *Doryphora* (7.2-16), *Drepanocarpus franckei* (7.2-21), *Echidiporites barbeitoensis* (7.2-43, 50), *Echimonocolpites* (7.2-50), *Echiperiporites akanthos* (7.2-50), *E. estelae* (7.2-43, 50), *Echites ettingshauseni* (7.2-44), *Echitricolporites maristellae* (7.2-43, 50), *E. mcneillyi* (7.2-43), *E. spinosus* (7.2-43), *Echitriporites trianguliformis* (7.2-43), *Empedoclea repando-serrata* (7.2-19a), *Engelhardtiopollenites* (7.2-45), *Enterolobium grandifolium* (7.2-21), *E. parvifolium* (7.2-21), *Ephedripites renzonii* (7.2-50), Ericaceae (6.1-10), *Ericipites* (7.2-43), *Erythrina* (6.1-10), *Erythrochyton grandifolium* (7.2-19a), *Erythroxylon cuneifolioides* (7.2-19b), *Escallonia wendtii* (7.2-22), *Eucalyptus patagonicus* (7.2-2), *Eugenia comparabilis* (7.2-33, 44), *Eugenia–Myrcia* (6.1-7, 8, 10), *Euphorbia* (?) (7.2-22), *Fagara miocenica* (7.2-44), *Fagus* [*Nothofagus*?] *megelhaenica* (7.2-19a), *F.* [*Nothofagus*?] *subferruginea* (7.2-14), *Faramea* (6.1-10), *F. miocenica* (7.2-19b), *Fenestrites longispinosus* (7.2-43), *F. spinosus* (7.2-43), *Ficus* cf. *betijoquensis* (7.2-33, 40), *F. culebrensis* (6.1-6), *F. procellanaria* (7.2-44), *F. talamancana* (7.2-33), *F. tressensii* (7.2-6), *F. winslowiana* (7.2-28a), *Flabellaria schwageri* (probably *Flagellaria*; 7.2-19a), *Gaylussacia tertiaria* (7.2-21), cf. *Glycydendron* (6.1-10), *Goeppertia ovalifolia* (7.2-19a), *G. spectalilis* (7.2-19a), *Gomphia firmifolia* (7.2-19a), *Gouatteria tenuinervis* (7.2-19a), *Goupioxylon stutzeri* (7.2-37), Gramineae (6.1-7, 9, 10), *Graminidites* (7.2-10, 13), *Grimsdalea magnaclavata* (7.2-43, 50), *Guarea* (6.1-10), *Guatteria culebrensis* (6.1-6; 7.2-28a), cf. *Guazuma* (6.1-7), *G. tertiaria* (7.2-28b), *Gyrocarpus miocenica* (7.2-41), *Haemadictyon tenuifolium* (7.2-19a), *Haloragacidites amolosus* (7.2-13), *H. harrisii* (7.2-13), *H. myriophylloides* (7.2-13), *Hampea–Hibiscus* (6.1-7, 10), *Hauya* (6.1-10), *Hedysarum bolivianum* (7.2-21), *Helianthus* type (4.1-22), *Heliconia elegans* (7.2-40, 44), *Hernandia tongi* (7.2-33), *Heterocolpites incomptus* (7.2-50), *H. rotundus* (7.2-50), *H. verrucosus* (7.2-50), *Hieronymia lehmanni* (6.1-6), *Hiraea oligocaenica* (6.1-6), *Hoffmannia protogaea* (7.2-19a), *Hygrophila* (5.1-20), *Hymenaea* (see Miocene amber), *Icica tertiaria* (7.2-19b), *Ilex* (6.1-7–10), *I. subtilinervis* (7.2-19a), *Ilexpollenites* (7.2-45, 50), *I. iliacus* (7.2-43), *I. margaritatus* (7.2-43), *Inga kugleri* (7.2-44), *I. ochseniusi* (7.2-21), *I. oligocaenica* (6.1-6), *Iriartites tumbezensis* (7.2-28a), *I. vaughani* (6.1-3), *Jandufouria seamrogiformis* (7.2-43, 50), cf. *Jatropha* (6.1-10), *Juglans linki* (7.2-29), *Jussitriporites* cf. *undulatus* (4.1-22), *Laetia transversonervis* (7.2-19a), *Laurelites doroteaensis* (7.2-15), *Laurinoxylon uniseriatum* (7.2-15), *Laurophyllum* (7.2-16), *L. actinodaphnoides* (7.2-19a), *L. kurtzi* (7.2-5), *Lecythidoanthus kugleri* (7.2-44), *Lecythis neriifolia* (7.2-19a), *Leguminosites canavaliformis* (7.2-44), *L. copaiferaeoides* (7.2-19a), *L. cuquensis* (7.2-41), *L. entadaformis* (7.2-40), *L. erythrinoides* (7.2-19a), *L. patagonicus* (7.2-19b), *L. silvensis* (7.2-44), *L. trinitensis* (7.2-44), *L. venezuelensis* (7.2-40), *Liliacidites* (7.2-45), *Lomatia occidentalis* (7.2-4), *L. patagonica* (7.2-4), *Lomatites occidentalis* (7.2-19b), *Lonchocarpus obtusifolius* (7.2-21), *Longaperites vaneendenburgi* (7.2-43), Loranthaceae (6.1-10), *Loxopterygium laplayensis* (end of 7.2-30), *Lymingtonia*? (7.2-10), *Machaerium eriocarpoides* (7.2-21), *Magnaperiporites spinosus* (7.2-43, 50), *Mallotus* (?) *platanoides* (7.2-19a), Malpighiaceae (6.1-7, 9, 10; 7.2-16), *Malvacarpus tertiarius* (7.2-19b), Malvaceae (6.1-9), *Malvacipollis spinulosa* (7.2-43), *M. subtilis* (7.2-10), *Malvacipolloides comodoroensis* (7.2-10, 13), *Manicaria* type (6.1-7–9), *Maravenites polyoratus* (7.2-43), *Margocolporites vanwijhei* (7.2-10, 43, 50), *Matayba* (6.1-7), *Mauritidites franciscoi* (7.2-43, 50), *Maytenus araucensis* (7.2-19a), *M. latifolioides* (7.2-19b), *M. magnoliaefolia* (7.2-19a), *M. trinitense* (7.2-44), Melastomataceae (6.1-10), *Melastomites miconioides* (6.1-6), *Melastomophyllum* (7.2-16), *Mello* (?) *cuquensis* (7.2-41), *Mespilodaphne colombiana* (7.2-33), *M. culebrensis* (6.1-6), *M. longifolia* (7.2-19a), *M. tumbezensis* (7.2-28a), *Mimosa arcuatifolia* (7.2-21), *M. montanoides* (7.2-21), *Mimosites* (7.2-21), *M. suteri* (7.2-41), *Mimusops anomala* (7.2-44), *M. miocenica* (7.2-44), *Mitraria* (7.2-16), *Momipites* (7.2-43), *Momisia asperulaformis* (7.2-28b), *M. iguanaeaformis* (7.2-28b), *Monoporites annulatus* (7.2-43, 50), *Monoporopollenites* (7.2-45), *Monosulcites* (7.2-45), *Mortoniodendron* (6.1-10), *Moschoxylun falcatum* (7.2-19a), *M. tenuinerve* (7.2-19a), *Multiareolites formosus* (7.2-43), *Multimarginites vanderhammeni* (7.2-43, 50), *Mutisiapollis viteauensis* (7.2-10), *Myrceugenellites maytenoides* (7.2-15), *Myrceugenia* (7.2-16), *Myrcia* (7.2-16), *M. acutifolia* (7.2-5), *M. chubutensis* (7.2-19b), *M.* (*Aulomyrcia*) *costatoides* (7.2-19a), *M. deltoidea* (7.2-19a), *M.* (*Cryptomyrcia*) *nitens* (7.2-19a), *M. reticulato-venosa* (7.2-14, 19a),

M. santacruzensis (7.2-5), *Myrciaria acuminata* (7.2-19a), *Myrciophyllum amgiguacoides* (7.2-19a), *Myrica banksioides* (7.2-20–22), *M. engelhardtii* (7.2-22), *M. mira* (7.2-19b), *M. potosina* (7.2-22), *M. wendtii* (7.2-21, 22), *Myricipites* (7.2-45), *Myricophyllum* (7.2-21), *Myristica fossilis* (7.2-19a), *Myristicophyllum panamense* (6.1-6), *Myrtaceidites* (7.2-10, 43), *M. mesonesus* (7.2-13), *M. verrucosus* (7.2-13), *Nectandra curvatifolia* (7.2-44), *N. kugleri* (7.2-44), *N. patagonica* (7.2-19b), *N. saltensis* (7.2-6), *N. silvarenaria* (7.2-44), *Nectandrophyllum* (7.2-19a), *Nothofagidites acromegacanthus* (7.2-10), *N. dorotensis* (7.2-13), *N. saraensis* (7.2-10, 13), *Nothofagus crenulata* (7.2-14), *N. gonzalezii* (7.2-16), *N. lanceolata* (7.2-14), *Ocotea* (7.2-16), *Omphales[a] ficiformis* (7.2-19a), *Orapollis* (7.2-10), *Orchideamasulites schlecteri* (7.2-43), *Ovidia* (7.2-16), *Pachydermites diederixi* (4.1-22; 7.2-43), Palmae (6.1-10), *Palmaepollenites* (7.2-45), *Palmocarpon bactrioides* (7.2-44), *P. fusiforme* (7.2-44), *Palmophyllum* (7.2-33, 44), *Palmoxylon palmacites* (6.1-6), *Passiflora* (?) *canfieldi* (7.2-22), *Patrisia eocenica* (7.2-19a), *Paullinia* (6.1-10), *Pelliceria* (6.1-9), *Peltophorum membranacea* (7.2-21), *Perfotricolpites digitatus* (7.2-43, 50), *Perisyncolporites pokornyi* (7.2-43, 50), *Persea* (7.2-14, 16), *P. coriacea* (7.2-33), *P. macrophylloides* (7.2-19a, 28a, 44), *P. microphylla* (7.2-19a), *P. preamericana* (7.2-44), *Petrea* (6.1-10), *Peumus clarki* (7.2-19b), *Phoebe* (7.2-16), *P. elliptica* (7.2-19a), *P. lanceolata* (7.2-19a), *Pilocarpus saavedrai* (7.2-19a), *Piperites* cf. *cordatus* (7.2-44), *Pithecolobium brittonianum* (7.2-23), *P. presaman* (7.2-28b), *P. tenuifolium* (7.2-44), *P. tertiarium* (7.2-21), *Platipodium potosianum* (7.2-21), *Plumiera alia* (7.2-44), *Poacites* (7.2-19b, 21), *Poluspissusites* (7.2-10), *Polyadopollenites* (7.2-9, 10, 50), *P. mariae* (7.2-43, 50), *Polycolpites* (7.2-45), *Polygalacidites* (7.2-45), *Polyorificites* (7.2-10), *Porlieria tertiaria* (7.2-22), *Posoqueria* (6.1-10), *P. columbiana* (7.2-33), cf. *Pouteria* (6.1-7), *Proteacidites* (7.2-10), *P. dehaani* (7.2-43), *P. triangulatus* (7.2-43, 50), *Proxaperites* (4.1-22), *P. cursus* (7.2-43), *P. minutus* (7.2-43), *P. operculatus* (7.2-43), *P. tertiaria* (7.2-43, 50), *Pseudobombax* (6.1-9, 10), *Psidium membranaceum* (7.2-19a), *Psiladiporites* (7.2-45), *P. minimus* (7.2-43, 50), *P. multiporus* (7.2-50), *P. redundatis* (7.2-50), *Psilamonocolpites amazonicus* (7.2-50), *P. medius* (7.2-43), *P. nanus* (7.2-50), *P. rinconii* (7.2-50), *Psilaperiporites minimus* (7.2-43, 50), *P. robustus* (7.2-43), *Psilastephanocolporites fissilis* (7.2-43, 50), *P. marinamensis* (7.2-50), *P. matapiorum* (7.2-50), *P. schneideri* (7.2-50), *Psilastephanoporites herngreenii* (7.2-50), *P. stellatus* (7.2-43), *Psilasyncolporites* (7.2-45), *Psilatricolpites acerbus* (7.2-50), *P. anconia* (7.2-50), *P. minutus* (7.2-50), *P.* cf. *papilioniformis* (7.2-50), *P. pulcher* (7.2-50), *P. simplex* (7.2-50), *Psilatricolporites* (7.2-45), *P. atalayensis* (7.2-50), *P. caribbiensis* (7.2-43), *P. costatus* (7.2-50), *P. crassus* (7.2-43, 50), *P. cyanus* (7.2-50), *P. devriesii* (7.2-43, 50), *P. divusus* (7.2-43, 50), *P. exiguus* (7.2-50), *P. garzonii* (7.2-50), *P. labiatus* (7.2-50), *P. maculosus* (7.2-43), *P. magniporatus* (7.2-50), *P. obesus* (7.2-50), *P. operculatus* (7.2-43, 50), *P. pachydermatus* (7.2-43), *P. silvaticus* (7.2-50), *P. transversalis* (7.2-43), *P. triangularis[tus]* (7.2-43, 50), *P.* cf. *varius* (7.2-50), *P. venezuelanus* (7.2-43, 50), *Psilatriporites corstanjei* (7.2-50), *P. desilvae* (7.2-50), *P. sarmientoi* (7.2-50), *Psittacanthus crassifolius* (7.2-19a), *Psychotria grandifolia* (7.2-19a), *Quercoidites* (7.2-45), *Quercus* (6.1-10), *Retibrevitricolpites* cf. *catatumbus* (7.2-43, 50), R. *triangularis* (7.2-43), R. *yavarensis* (7.2-50), *Retimonocolpites absyae* (7.2-50), R. *longicolpatus* (7.2-43, 50), R. *maximus* (7.2-50), R. *retifossulatus* (7.2-43, 50), *Retistephanoporites angelicus* (7.2-50), R. *crassiannulatus* (7.2-43, 50), *Retitricolpites* (7.2-45), R. *amapaensis* (7.2-43, 50), R. *antonii* (7.2-50), R. *caquetanus* (7.2-50), R. *colpiconstrictus* (7.2-50), R. *depressus* (7.2-50), R. *lalongatus* (7.2-50), R. *lewisii* (7.2-50), R. *lorentae* (7.2-50), R. cf. *maledictus* (7.2-50), R. cf. *maturus* (7.2-50), R. *simplex* (7.2-43, 50), R. *tuberosus* (7.2-50), R. *wijningae* (7.2-50), *Retitricolporites* (7.2-43), R. cf. *amazonensis* (7.2-43), R. cf. *brevis* (7.2-43), R. *caputoi* (7.2-50), R. *crassicostatus* (7.2-50), R. *crassopolaris* (7.2-50), R. *ellipticus* (7.2-50), R. *guianensis* (7.2-43, 50), R. *hispidus* (7.2-43, 50), R. *irregularis* (7.2-43, 50), R. *kaarsii* (7.2-50), R. *latus* (7.2-50), R. *leticianus* (7.2-50), R. *medius* (7.2-50), R. *milnei* (7.2-50), R. *oblatus* (7.2-50), R. *poriconspectus* (7.2-50), R. *pygmaeus* (7.2-50), R. *santaisabelensis* (7.2-50), R. *solimoensis* (7.2-50), R. *ticuneorum* (7.2-50), R. *wijmstrae* (7.2-50), *Retitriporites dubiosus* (7.2-50), *Rhamnidium miocenicum* (7.2-44), R. (?) *patagonicum* (7.2-19b), R. *preglabrum* (7.2-19b), *Rheedia miocenica* (7.2-33, 44), *Rhizophora* (6.1-7–10), R. *boweni* (7.2-40), *Rhoipites* (7.2-45), R. *baculatus* (7.2-10), R. *cienaguensis* (7.2-10, 13), *Rondeletia goldmani* (6.1-6), cf. *Rourea* (6.1-7), Rubiaceae (6.1-9), *Rubiacites ixoreoides* (6.1-6), *Rugutricolporites arcus* (7.2-50), *Ruprechtia braunii* (7.2-21), *Sabal ochseniusi* (7.2-19a), *Sabalites* (7.2-40), *Sabicea* (6.1-7), *S.* (?) *elliptica* (7.2-19a), *Sapindus acuminatus* (7.2-19a), *S. argentinus* (7.2-19b), *Sapium* (6.1-7), *Sapotaccoidaepollenites* (7.2-45), *Scabratricolporites planetensis* (7.2-43), *Scabratriporites redundans* (7.2-50), *Schinopsis? dubia* (7.2-5), *S. patagonica* (7.2-19b), *Schinus herbstii* (7.2-6), *Schmidelia bejucensis* (6.1-6), *S. eduliforma* (7.2-19b), *S. graciliforma* (7.2-19b), *S. proedulis* (7.2-19b), *Senipites patagonica* (7.2-10), *Senna* (7.2-16), *Serjania* (6.1-10), *Sideroxylon mastichodendroides* (7.2-41, 44), *Simarouba miocenica* (7.2-40), *Sophora salvadorana* (7.2-40), *Sparganiaceaepollenites barungensis* (7.2-13), *Spinozonocolpites echinatus* (7.2-43), *Spirosyncolpites spiralis* (7.2-50), *Stenospermation columbiense* (7.2-28a), *Stephanocolpites evansii* (7.2-43, 50), *Sterculia patagonica* (7.2-19b), cf. *Stillingia* (6.1-10), *Striacolporites tenuissimus* (7.2-43), *Striatricolpites catatumbus* (7.2-43, 50), *Striatricolporites gamerroi* (7.2-10, 13), *Strychnos mirhojana* (7.2-19b), *Styrax acuminatiformis* (7.2-19b), *S. coriacea* (7.2-19a), *S. glabratoides* (7.2-19a), *S. lanceolata* (7.2-28a), *S.* (?) *lehneri* (7.2-44), *Sweetia tertiaria* (7.2-20, 21), *Swertia* (*Galactia*) *tertiaria* (7.2-22), *Symplocos* (6.1-10), *Syncolporites anibalii* (7.2-50), *S.* cf. *incomptus* (7.2-50), *S. poricostatus* (7.2-50), *Synechanthus* type (6.1-7, 9), *Taenioxylon multiradiatum* (6.1-6), *Tapirira lanceolata* (7.2-28a, 33), *T. trinitiana* (7.2-44), *Tecoma serrata* (7.2-19a), *Terminalia antiqua* (7.2-22), *T. trinitense* (7.2-44), *Tetracera elliptica* (7.2-19a), *T. patagonica* (7.2-19b), *T. rhamnoides* (7.2-19a), *T. tertiaria* (7.2-28b), *Tetracolporites spectabilis* (7.2-10), *Tetraplandra longifolia* (7.2-19a), *Tetrapollis* (7.2-45), *Tetrorchidium* (6.1-7), *Thevetia angustifolia* (7.2-19a), *Thouinia philippii* (7.2-19a), *Ticorea foetidoides* (7.2-19a), *Tipuana ecuadoriana* (end of 7.2-30), *Trema micranthaformis* (7.2-28b), *Trichilia hirtaformis* (7.2-44), *Trichotomocolpites* (7.2-43), *Trichotomosulcites* (7.2-50), *Tricolporites reticulatus* (7.2-13), *T. trioblatus* (7.2-13), *T.* sp. 1 (7.2-13), *Trigonia varians* (7.2-28a, 40), *Triumfettia irregulariter-serrata* (7.2-19a), *Trivestivulopollenites* (7.2-13), *Tublifloridites antipodica* (7.2-10, 13), *T. simplis* (7.2-13), *T. viteauensis* (7.2-13), *T.* sp. (7.2-13), *Utricularia* (6.1-9, 10), *Vallea*

prepubescens (7.2-28b), *Venezuelites globoannulatus* (7.2-43), *Verrutricolporites* (7.2-45), *V. rotundiporus* (7.2-43, 50), *Vochysia dura* (7.2-19a), *V. retusifolia* (7.2-28a), *Weinmannia* (7.2-16), *W. brittoni* (7.2-21), *Zanthoxylon* (7.2-14), *Z. inaequabile* (7.2-19a), *Z. tenuifolium* (7.2-19a), *Zonocostites duquei* (7.2-50), *Z. ramonae* (7.2-43). Incertae sedis: *Antholithes quinquepartia* (7.2-21), *Carpolites cycaeformis* (7.2-19a), *C. guiliemaeoides* (7.2-19a), *C. ovoideus* (7.2-21), *Carpolithus bivascularis* (7.2-19b), *C. mirhojanus* (7.2-19b), *C. patagonicus* (7.2-19b), *Leguminosites* (?) *globularis* (7.2-21), *Mimosites linearis* (7.2-21), *Phyllites* (7.2-5, 16, 33), *P. acuto-serratus* (7.2-19a), *P. alsodeiaecoides* (7.2-19a), *P. aspidospermaeoides* (7.2-19a), *P. banisteriaeoides* (7.2-19a), *P. coccolobaeafolia* (7.2-19a), *P. cycaeformis* (7.2-19a), *P. franckii* (7.2-20–22), *P. repandus* (7.2-19a), *P. sauraujaeoides* (7.2-19a), *P. sloaneaformis* (7.2-19b), *P. ternstroemiaeoides* (7.2-19a), *P. triplarioides* (7.2-19a), *P.* sp. 1–5 (7.2-16).

Mio–Pliocene, Pliocene, Plio–Pleistocene

Fungi

Caenomyces braziliensis (7.2-46), *Hiospira* (7.2-39), *Hysterites ellipticus* (7.2-31), *Microthyrium* (6.1-13; 7.2-39), *Neurospora* (7.2-39), *Sphaerites consociatus* (7.2-31), *S. punctiformis* (7.2-31), *S. sparsus* (7.2-31), *Xylomites immersus* (7.2-31).

Algae

Botryococcus (7.2-8), *Operculodinium* (6.1-11, 12), *Pediastrum* (7.2-8), cf. *Spirogyra* (7.2-39).

Bryophyta

aff. *Breutelia* (7.2-39), aff. Hookeriaceae (7.2-39), aff. *Lejeunea* (7.2-39), *Muscites* (7.2-30), *Phaeoceros* (6.1-13), aff. *Prionolejeunea* (7.2-39), *Sphagnum* (7.2-39), aff. Thuidiaceae (7.2-39).

Ferns and allied groups

cf. *Acrostichum* (6.1-12, 15), *A. linearifolium* (7.2-23, 25), *Adiantum* (6.1-15), *Alsophila* (4.1-26), cf. *Antrophyum* (6.1-12, 14), *Azolla* (7.2-8, 39), *Ceratopteris* (4.1-26; 6.1-15), *Cnemidaria* (4.1-26; 6.1-13; 7.2-27), *Crassoretitriletes vanraadschoovenii* (7.2-39), *Cyathea* (4.1-26; 7.2-27), *C. colombiensis* (7.2-36), *Cyatheacidites annulatus* (7.2-8), *Danaea* (7.2-27, 39), *Dicranopteris* (4.1-26), *Elaphoglossum carrioni* (7.2-30), *Equisetum* (6.1-15), *Filicites lojanus* (7.2-30), *Goniopteris* (7.2-25), *G. cochabambensis* (7.2-30, 34), *G. lojana* (7.2-30), *Grammitis* (7.2-27), *Gymnogramma* (7.2-23, 25), *Hemitelia branneri* (7.2-46), cf. *Hymenophyllum* (6.1-13; 7.2-27), *Ischyosporites areapunctatis* (7.2-8), *Isoetes* (6.1-15; 7.2-27), *Lomariopsis* (4.1-26), *L. tertiaria* (7.2-23, 25), *Lophosoria* (6.1-13), *Lycopodium* (4.1-26; 6.1-11, 13; 7.2-27), *Lygodium bifidium* (7.2-30), *Meniscium* [*Thelypteris*] *wolfi* (7.2-32), monolete fern spores (4.1-26), *Muricingulisporis chenquensis* (7.2-8), *Pecopteris* (7.2-23; undeterminable fragment of Paleozoic fern-like foliage), *Pityrogramma* (4.1-26; 6.1-13), Polypodiaceae (6.1-15), *Polypodiisporites* (4.1-22), Polypodiales (7.2-39), *Polypodium* (6.1-15), *Polystichum bolivianum* (7.2-23–25), *Psilotum* (4.1-26), *Pteris* (6.1-13, 14; 7.2-27), cf. *Rhipidopteris–Elaphoglossum* (6.1-15), *Salvinia* (6.1-15), *S. lechmanni* (7.2-32), *Selaginella* (4.1-26; 6.1-11–13; 7.2-39), *Sphaeropteris–Trichipteris* (4.1-26), trilete fern spores (4.1-26).

Gymnosperms

Abies (4.1-26; 6.1-15), Araucariaceae (7.2-8), *Decussocarpus* (7.2-39), *Equisetosporites claricristatus* (7.2-8), *Picea* (4.1-26; 6.1-11), *Pinus* (4.1-26; 6.1-11, 12, 15), Podocarpaceae (7.2-8), *Podocarpus* (4.1-26; 6.1-13; 7.2-39), *P. boliviensis* (7.2-25), *P. fossilis* (7.2-23–25), *Podocarpus–Prumnopitys* (7.2-27), *Zamia* (7.2-30).

Angiosperms

Acacia (4.1-26; 6.1-15), *A. dimidiato-cordata* (7.2-23, 25), *A. tenuifolia* (7.2-23, 25), *A. uninervifolia* (7.2-23–25), *Acacioxylon o'donellii* (7.2-7), cf. *Acridocarpus* (6.1-15), *Acrodiclidium chartaceum* (7.2-32, 36), *Aeschynomene bolivianum* (7.2-23, 25), *Alchornea* (4.1-26; 6.1-13, 14), *A. swartzi* (7.2-30), *Alfaroa–Oreomunnea* (4.1-26; 6.1-11, 12), cf. *Alibertia* (4.1-26), Alismataceae (7.2-39), *Allophylus* (4.1-26), *Alnus* (4.1-26), *Ambrosia* (4.1-22), *Amicia antiqua* (7.2-23–25), *Anacardites braziliensis* (7.2-46), cf. *Anacardium* (7.2-39), *An(n)ona* (6.1-15), *A. carnavalii* (7.2-49), *A. costaricana* (6.1-5), *A. lamegoi* (7.2-49), *A. oliveirae* (7.2-49), *A. sarvariana* (7.2-42), *Anthurium* (7.2-39), *Apocynophyllum potosianum* (7.2-23, 25), *Arecipites subverrucatus* (7.2-8), *Arrabidaea* (7.2-47), *Artanthe geniculatoides* (7.2-30, 31), *Artemisia* (4.1-22), cf. *Asplundia* (7.2-39), *Astrocaryum* (4.1-26; 7.2-39), cf. *Attalea* (4.1-26), *Bambusium stubeli* (7.2-32, 36), *Banisteria* (6.1-15), *B. aceroides* (7.2-30, 31), *B. oblongifolia* (7.2-47), cf. *Banisteriopsis* (6.1-13), *Bauhinia* (6.1-15), *B. ecuadorensis* (7.2-30), *B. potosiana* (7.2-23, 25), *Baumannipollis variaperaturatus* (7.2-8), cf. *Bernardia* (4.1-26), *Bignonia tertiaria* (7.2-30, 34), Bignoniaceae (6.1-15), Bombacaceae (6.1-13), *Bombax aramariensis* (7.2-46), *B. retusifolium* (7.2-30, 31), *Borreria* (4.1-26), *Bothriospora witti* (7.2-32, 36), cf. *Brahea* (4.1-26), *Bravaisia* (4.1-26), cf. *Bredemeyera* (4.1-26), *Brownea* (7.2-39), *Bucida buceras* (6.1-15), *Bumelia cuneatoides* (7.2-46), *B. lojana* (7.2-30), *B. marahiana* (7.2-46), *Bursera* (4.1-26), *Bue(y)ttneria* (4.1-26), *B. cinnamomifolia* (6.1-5; 7.2-32, 36), *Caesalpinia* (6.1-12), *C. echinataformis* (7.2-47), *C. gmehlingi* (7.2-23, 25), *C. potosianus* (7.2-23, 25), *C. sessilifolioides* (7.2-23, 25), *C. subdimidiata* (7.2-30, 31), *Calliandra obliqua* (7.2-23, 25), *C. ovatifolia* (7.2-23, 25), *Callitriche* (7.2-39), *Calophyllites mesaensis* (7.2-36), *Calophyllum calabaformis* (7.2-42), *Calyptranthes marahiensis* (7.2-46), *Camphoromaea speciosa* (7.2-30, 31), *Canella winterianafolia* (7.2-46), *Capparis multinervis* (7.2-23, 25), *C. verrucosafolia* (7.2-30), *Carex* (7.2-39), *Carya* (6.1-15), *Casearia* (4.1-26), *Cassia aguaytensis* (7.2-34), *C. bassleri* (7.2-30), *C. bigidulifolia* (7.2-23), *C. chrysocarpoides* (7.2-23, 25), *C. cristoides* (7.2-23, 25), *C. cultrifoliaformis* (7.2-23, 25), *C. dimidiato-linearis* (7.2-30, 31), *C. fonescana* (7.2-47), *C. franckei* (7.2-23, 25), *C. leptocarpoides* (7.2-42), *C. ligustrinaformis* (7.2-23–25), *C. linearifolia* (7.2-30, 31), *C. longifolia* (7.2-30, 31), *C. marahiana* (7.2-46), *C. membranacea* (7.2-23, 25), *C. obscura* (7.2-23, 25), *C. obtusatafolia* (7.2-47), *C. rigidulifolia* (7.2-21, 23, 25), *C. singewaldi* (7.2-23–25), *C. wendtii* (7.2-23, 25), *C. zuliana* (7.2-34), cf. *Catopsis* (7.2-39), *Cavanillesia* (7.2-27), *Cecropia* (7.2-39), *Cedrela* (4.1-26; 6.1-15), *C. campbeli* (7.2-47), *C. preodorata* (7.2-42), cf. *Ceiba* (6.1-15), *Celtis* (4.1-26; 6.1-15), *Ceratophyllum demersum* (6.1-15), cf. *C. llerenae* (6.1-15), cf. *Chamaedorea* (4.1-26), chenoam (4.1-26; 6.1-15), *Chenopodipollis chenopodiaceoides* (7.2-8), cf. Chrysobalanaceae (7.2-39), *Chrysobalanus precuspidatus*

(7.2-46), *C. preicaco* (7.2-46), *Chrysophyllum cainitoformis* (7.2-42), *C. rufoides* (7.2-32, 36), *Cinnamomum incertum* (7.2-46), *Citharexylon retiformis* (7.2-32, 36), *Citrophyllum bahiensis* (7.2-46), *Cleyera* (4.1-26), *Coccoloba* (4.1-26), *Coccolobis preuvifera* (7.2-47), *C. tertiaria* (7.2-46), *Combretum fonsecanensis* (7.2-47), *C. jacquinifolia* (7.2-42), *Combretum–Terminalia* (4.1-26), *Comocladia* (4.1-26), Compositae (4.1-26; 6.1-11–13, 15; 7.2-27, 39), *Condaminea grandifolia* (7.2-32, 36), cf. *Connarus* (7.2-39), cf. *Copaifera* (6.1-15), *C. corocoriana* (7.2-23–25), *C. potosiana* (7.2-23, 25), *Corsinipollenites atlantica* (7.2-8), cf. *Cotinus coggygria* (6.1-15), *Couratari tertiaria* (7.2-30, 31), *Couroupita ovata* (7.2-46), *C. tertiaria* (7.2-30), *Coussapoa* (7.2-39), *C. carrioni* (7.2-30), *Coussapoites portae* (7.2-36), *C.* aff. *veracruziana* (7.2-36), *Crudioxylon pinalense* (7.2-38), *C.* sp. (7.2-38), *Cupania* (4.1-26), *Cuphea* (4.1-26), *C. antiqua* (7.2-23, 25), *Cusparia yacuibana* (7.2-26), cf. *Cyclanthus* (7.2-39), Cyperaceae (4.1-26; 6.1-11, 12, 15), *Cyperaceaepollis neogenicus* (7.2-8), *Cypselites potosianus* (7.2-23, 25), *Dalbergia antiqua* (7.2-23–25), *D. chartacea* (7.2-23, 25), *D. ettinghauseni* (7.2-46), *D. potosiana* (7.2-23, 25), *Daphnopsis* (4.1-26), *Desmodium ellipticum* (7.2-23, 25), *Dichapetalum* (4.1-26), *Dodonaea vera* (7.2-46), *D. viscosaformis* (7.2-24, 25), *Drepanocarpus franckei* (7.2-23–25), *Duvaua pliocenica* (7.2-25), *Ecclinusa* (7.2-39), *Elatine* (7.2-39), *Eleocharis* (7.2-39), *Enckea columbrinoides* (7.2-30), *Endlicheria rhamnoides* (7.2-31), cf. *Enterolobium* (6.1-15), *E. grandifolium* (7.2-23–25), *E. parvifolium* (7.2-23, 25), Ericaceae (6.1-13; 7.2-27), *Erythrochiton bahiense* (7.2-46, 47), *Escallonia wendtii* (7.2-23, 25), *Eugenia camparabilis* (7.2-42), *E. ovalifolia* (7.2-30, 31), *Eugenia–Myrcia* (4.1-26; 6.1-13, 15), *Euphorbia* (?) (7.2-23, 25), cf. *Evodianthus* (7.2-39), *Exostema precaribaeum* (7.2-30), Fagaceae (7.2-8), *Fagara dentatafolia* (7.2-46), *F. formosa* (7.2-46), *Faramea* (4.1-26), *Festuca* (7.2-23, 25), *Ficus* (6.1-15), *F. aramaryensis* (7.2-46), *F. betijoquensis* (7.2-34), *F.* cf. *cotinifolius* (6.1-15), *F. laqueata* (7.2-32, 36), *F. mamilliferafolia* (7.2-46), *F. talamancana* (6.1-5), *Freziera* (7.2-39), *Gaylussacia ovata* (7.2-25), *G. tertiaria* (7.2-23, 25), *Geissanthus brittoni* (7.2-42), *Glencopollis ornatus* (7.2-8), cf. *Glycydendron* (6.1-13), *Goeppertia–Goppertia tertiaria* (6.1-5), *G. subherbacea* (7.2-32, 36), *Gouania firma* (7.2-32, 36), *G. membranacea* (7.2-32, 36), Gramineae (4.1-26; 6.1-11, 12, 15; 7.2-23, 27), Gramineae–Cyperaceae (6.1-15), *Graminidites* (7.2-8), *Guaiacum pliocenicum* (7.2-46), *Guarea* (4.1-26), *Gunnera* (7.2-39), *Gustavia* (4.1-26), *Gyminda latifolioides* (7.2-46), cf. *Haematoxylon* (6.1-15), cf. *Hamamelis* (6.1-15), *Hampea–Hibiscus* (4.1-26), *Hedyosmum* (4.1-26), *Helianthus* (4.1-22), *Heliconia* (6.1-5), *H. bahiana* (7.2-47), *Heliconiophyllum elegans* (7.2-36), *H. falanense* (7.2-36), *Hernandia* (7.2-42), *Hieronymia lehmanni* (6.1-5; 7.2-31), *Hippocratea–Pristimera* (7.2-39), cf. *Hippuris* (6.1-15), *Hiraea* (4.1-26; 6.1-13, 15), *H. cyclosperma* (7.2-30, 31), *Hirtella lojana* (7.2-30), *Hoffmannia boliviana* (7.2-25), *Homalanthus prenutans* (7.2-47), *Huberia preovalifolia* (7.2-46), *Humiriastrum* (7.2-39), *Ilex* (4.1-26; 6.1-13, 14, 15; 7.2-27), *I. arcinervis* (7.2-32, 36), *I. bahiana* (7.2-46), cf. *Inga* (6.1-15), *I. engelhardti* (7.2-30), *I. kugleri* (7.2-42), *I. latifolia* (7.2-31), *I. lojana* (7.2-30, 34), *I. myrianthafolia* (7.2-46), *I. ochseniusi* (7.2-23, 25), *I. ovalifolia* (7.2-31), *I. reissi* (7.2-32, 34, 36), *I. sheroliensis* (6.1-5), *Iresine* (4.1-26; 6.1-11), *Jacaranda potosiana* (7.2-23, 25), *J. tertiaria* (7.2-46, 47), *Jambosa lanceolata* (7.2-32, 36), *Juglans* (4.1-26; 6.1-11, 15), *Juncus* (7.2-39), *Justicia* (4.1-26), cf. *Karwinskia* (6.1-15), *Kielmeyera tertiaria* (7.2-46), *Labatia fonsecana* (7.2-47), *Lacmellea* (6.1-14), *Lactoris* (7.2-8), *Laetia* (4.1-26), *Laguncularia* (4.1-26), *Laurophyllum rigidum* (7.2-32), *Leguminosites acaciaeformis* (7.2-31), *L. bahiensis* (7.2-46), *L. braziliensis* (7.2-46), *L. caseareana* (7.2-34), *L. cassioides* (7.2-30, 31), *L. engelhardti* (7.2-30), *L.* (?) *globularis* (7.2-23, 25), *L. grandis* (7.2-30, 31), *L. hymenaeoides* (7.2-46), *L. machaerioides* (7.2-31, 46), *Leptolobium eonitens* (7.2-46), *Liquidambar* (4.1-26), *Lisianthius* (6.1-13), *Lonchocarpus engelhardti* (7.2-30), *L. obtusifolius* (7.2-23, 25, 31), *Ludwigia* (4.1-26; 6.1-11; 7.2-39), *Luhea tertiaria* (7.2-30, 31), Lythraceae (7.2-39), cf. *Machaerium* (7.2-39), *M. eriocarpoides* (7.2-23–25), *M. milleri* (7.2-23, 25), cf. *Macoubea* (7.2-39), *Macrolobium tenuifolium* (7.2-30, 31), *Malpighia* (4.1-26), *Malvacipolloides comodoroensis* (7.2-8), *Marsdenia macrophylla* (6.1-15), *Matayba* (4.1-26), *Maytenus anzoateguiensis* (7.2-42), *M. dasycladoides* (7.2-46), *M. trinitense* (7.2-42), *Maximiliana* type (4.1-26), Melastomataceae (6.1-13, 15; 7.2-39), *Melastomites* (7.2-30), *Meliosma* (4.1-26), *Melochia carrioni* (7.2-30), *Mespilodaphne acrensis* (7.2-34), *M. lojana* (7.2-30), cf. *Mezia* (?) type (4.1-26), *Miconia ettinghauseni* (7.2-46), *M. prealbicans* (7.2-46), *Milfordia argentina* (7.2-8), *Mimosa* (4.1-26), *M. arcuatifolia* (7.2-23–25), *M. montanoides* (7.2-23, 25), *Mimosites engelhardti(i)* (7.2-23–25), *M. linearis* (7.2-25), *Mimusops miocenica* (7.2-30, 42), *Momisia ecuadorensis* (7.2-30), *M. iguanaeaformis* (7.2-30), *Moquilea stubeli* (7.2-32, 36), *Mortoniodendron* (4.1-26), *Moschoxylon tenuinerve* (7.2-32, 36), *Multiaerolites formosus* (4.1-22), *Multisiapollis viteauensis* (7.2-8), *Muntingiophyllum calaburoides* (7.2-36), *Musophyllum elegans* (7.2-32), *Myrcia antediluviana* (7.2-30, 31), *M. cajamarcana* (7.2-30), *M. rostrataformis* (7.2-46), *Myrica* (4.1-26; 6.1-15), *M. banksioides* (7.2-23, 25), *M. engelhardtii* (7.2-23), *M. wendtii* (7.2-23), *Myricaria tenuifolia* (7.2-30, 31), *Myricophyllum* (7.2-23, 25), *Myristica fossilis* (7.2-30, 31), *Myroxylon* cf. *balsamum* (6.1-15), *Myrsine braziliana* (7.2-47), *M. ciliatafolia* (7.2-46), *M. eomyricoides* (7.2-30), Myrtaceae (6.1-15), *Myrteola potosiana* (7.2-23, 25), *Nectandra areolata* (6.1-5; 7.2-32, 36), *N. curvatifolia* (7.2-32, 36, 42), *N. reissi* (7.2-30, 32, 36), *N. woodringi* (6.1-5), Nymphaeaceae (7.2-39), cf. *Ocotea* (6.1-15), *O.* cf. *rubra* (7.2-36), cf. *Oreopanax* (7.2-27), *Osteomeles pliocenica* (7.2-24, 25), *Oxandra emygdiana* (7.2-49), *Palmacites* (7.2-32), Palmae (6.1-11, 12, 14, 15; 7.2-23, 27, 30, 39), *Palmocarpon geonomoides* (6.1-4), *Palmophyllum* (7.2-23, 25), *Paraprotium* (7.2-39), *Parinari* (7.2-39), *Passiflora* (4.1-26), *P. canfieldi* (7.2-23, 25), cf. *Paullinia* (4.1-26), *Pelliceria* (6.1-14), cf. *Peltophorum membranaceum* (7.2-23–25), *Peperomia* (6.1-15), *Pereskia* (7.2-27), cf. *Persea* (6.1-15), *P. coriacea* (7.2-30, 32, 36), *P. elliptica* (7.2-32, 36), *P. elongata* (7.2-32, 36), *P. macrophylloides* (7.2-32, 36, 42), *P. preamericana* (7.2-42), *Phorodendron fossile* (7.2-30, 31) *Phragmites* (7.2-23, 25), *Pilocarpus prepinnatifolius* (7.2-46), *Piperites cordatus* (6.1-5), *P. potosiensis* (7.2-25), *P. quinquecostatus* (6.1-5), *Pisonia branneri* (7.2-46), *P. witti* (7.2-30), cf. *Pithecolobium* (6.1-15), *P. brittonianum* (7.2-23, 25), *P. ecuadorensis* (7.2-30), *P. presaman* (7.2-30, 34), *P. tenuifolium* (7.2-32, 36, 42), *P. tertiarium* (7.2-23, 25), cf. *Platypodium potosianum* (7.2-23, 25), *Plumiera*

rubraformis (7.2-46), *P. tertiaria* (7.2-30), *Poacites* (7.2-23, 25), *P. magnus* (7.2-30, 31), Polygonaceae (6.1-14, 15), cf. *Polygonum* (7.2-39), *Populus* (4.1-26), *Porlieria tertiaria* (7.2-23, 25), *Posoqueria columbiana* (7.2-30, 32), cf. *Potamogeton* (6.1-15), cf. *Preskia* (7.2-27), *Pristimera* (see *Hippocratea–Pristimera*), cf. *Protium* (4.1-26), cf. *Psidium* (6.1-15), *P. cuneatifolium* (7.2-46), cf. *Psittacanthus* (6.1-14), cf. *Psychotria* (7.2-39), cf. *Pterocarpus* (6.1-15), cf. *Pterocarya* (?) (6.1-15), *Pterogyne oblongifolium(-lia)* (7.2-30, 31), *Quercus* (4.1-22, 26; 6.1-11, 15), *Q.* cf. *crassifolia* (6.1-15), *Quintiniapollis striatulosa* (7.2-8), *Rajania* (4.1-26), *Ranunculus* (7.2-39), *Retimonocolpites retifossulatus* (7.2-39), *Rhamnidium elaeocarpoides* (7.2-30), R. *miocenicum* (7.2-44), *Rheedia* (7.2-34, 39), R. *pliocenica* (7.2-46), R. *preacuminata* (7.2-42), *Rhizoma graminis* (7.2-32, 36), *Rhizophora* (4.1-26; 6.1-12, 13), *Rhoipites cienaguensis* (7.2-8), cf. *Rhus* (6.1-15), *Rollinia tertiaria* (7.2-46), cf. Rubiaceae (7.2-39), *Rubiacites nummularioides* (7.2-23–25), *Rubus* (7.2-39), *Ruprechtia braunii* (7.2-23–25, 30), *Sabicea* (6.1-14), *S. asperifolia* (7.2-32), *Sacoglottis* (7.2-39), *S. tertiaria* (7.2-39), cf. *Salix* (6.1-15), *Sapindus presaponaria* (7.2-46, 47), cf. *Sapium* (4.1-26), cf. Sapotaceae (4.1-22; 6.1-15), cf. *Scirpus* (7.2-39), *Scleria wolfi* (7.2-30, 31), cf. *Securidaca* (4.1-26), *Senipites patagonica* (7.2-8), *Serjania tertiaria* (7.2-30), *Simaruba whitei* (7.2-46), *Siparuna preguayensis* (7.2-47), *Smilax* (4.1-26), Solanaceae (7.2-39), *Sparattanthelium pliocenicum* (7.2-30, 34), *Sparganiaceaepollenites barungensis* (7.2-8), *Sparganium* (7.2-8), *Spathiphyllum* (4.1-26), *Spondias mirifica* (7.2-46), *Stenolobium rhomboidalis* (7.2-30, 31), *Stenospertatium columbiense* (7.2-32, 36), cf. *Stillingia* (4.1-26), *Struthanthus* (4.1-26; 6.1-14), cf. *Strychnos* (6.1-15), *Styrax lanceolata* (7.2-32, 36), *S. lehneri* (7.2-42), *S. preferrugineum* (7.2-46), *S. styracioides* (7.2-30), *Sweetia tertiaria* (7.2-23, 25), *Symphonia* (4.1-26; 6.1-14), *Symplocos* (6.1-15; 7.2-39), cf. *S. limoncillo* (6.1-15), *Talisia ecuadoriana* (7.2-30), *Tapiria lanceolata* (7.2-30, 31, 42), *Tecoma grandidentata* (7.2-32, 36), *Terebraria* (4.1-26), *Terminalia antiqua* (7.2-23, 25), *T. maxima* (7.2-47), *T. singewaldi* (7.2-23–25), *Tetracera tertiaria* (7.2-30), *Tetrorchidium* (4.1-26; 7.2-27), *Thalictrum* (4.1-26), *Theobroma tertiaria* (7.2-42), *Thoracocarpus* (7.2-39), *Tibouchina dolianitii* (7.2-48), *T. santosii* (7.2-48), cf. *Tithymalus* (4.1-26), *Tournefortia* (4.1-26), *Trichilia branneri* (7.2-46), *T. hirtaformis* (7.2-30, 42), *Tricolpites trilobatus* (7.2-8), *Trigonia varians* (7.2-30, 32, 36, 42), *Triptolemea tertiaria* (7.2-34, 47), *Tubulifloridites antipodica* (7.2-8), *Turpinia* (7.2-39), *Ulmus* (4.1-26; 6.1-11, 12, 15), *Urtica* (7.2-39), *Utricularia* (4.1-26), *Vaccinium pontzuelum* (7.2-24, 25), *Vantanea* (7.2-39), *Vochysia acuminatafolia* (7.2-46), *V. ferruginoides* (7.2-30, 31), *V. retusifolia* (7.2-32, 36), *V. witti* (7.2-31), *Weinmannia brittonii* (7.2-23, 25), *W. potosina* (7.2-23, 25), *Xyris* (7.2-39), *Zanthoxylum* (7.2-39). Incertae sedis: *Antholithus bahiana* (7.2-46), *A. kielmeyerana* (7.2-46), *A. quinquepartita* (7.2-23, 25), *Carpolithus badieroides* (7.2-46), *C. bahiensis* (7.2-46), *C. baulti* (7.2-24), *C. engelhardti(i)* (7.2-23, 25), *C. viornaformis* (7.2-23, 25; Ranunculaceae?), *C.* sp. 1-5 (7.2-23, 25), *Phyllites abutoides* (7.2-32, 36), *P. bahiana* (7.2-46), *P. celastrinoides* (7.2-30, 31), *P. columbrinoides* (7.2-31), *P. costaricensis* (6.1-5), *P. gouareoides* (7.2-30, 31), *P. marahiensis* (7.2-46), *P. nymphaeacites* (7.2-25), *P. strychnoides* (7.2-32, 36), *P. styracoides* (7.2-31), *P. vochysioides* (7.2-32, 36).

Tertiary (undifferentiated)

Angiosperms

Acacioxylon (4.1-41), *Juglans* (4.1-42), *Karatophyllum bromelioides* (see text, Costa Rica), *Palmacites berryanum* (see text, Costa Rica), *Palmoxylon* (4.1-41); *Colombicarpum biloculare*, *Saccoglottis costata* (Reid, 1933).

Quaternary

[Note: in Table 6.1, references for the Quaternary are listed and numbered separately]

Fungi

Asteria (7.6-20), *Athelia* (7.6-20), fungal spores (6.1-2, 8, 16), *Gaeumannomyces* cf. *caricis* (7.6-20), *Gelasinosperma adjuncta* (7.6-20), *G. retispora* type (7.6-20), *Helicoon pluriseptatum* (7.6-20), *Hiospira* (7.6-20), *Micropeltis* (7.6-20), *Microthyrium* (7.6-20), *Neurospora* (7.6-20), *Pleospora* (7.6-20), *Sphaerodes* (7.6-20), *Spirotremesporites ecuatorialis* (7.6-20), *S. simplex* (7.6-20), cf. *Stemphyllum* (7.6-20), *Tetraploa aristata* (7.6-20), *Tilletia sphagni* (7.6-20), *Ulospora* (7.6-20).

Algae and allied groups/Protista

Amphitrema flavum (7.6-20), *Arcella arenaria* (Protista, 7.6-20), *A. brasiliensis* (7.6-20), *A. catinus* (7.6-20), *A. discoides* (7.6-20), *A. polypora* (7.6-20), *Assulina seminulum* (7.6-20), *Botryococcus* (4.1-32; 5.1-23; 6.1-2, 4, 8, 16; 7.6-8, 21, 22, 24, 25, 29, 33), *B. braunii* (7.6-20), *Chlamydomonas* (7.6-31), *Coelastrum* (7.6-25), *C. reticulatum* (7.6-20), *Cosmarium* (7.6-20), *Debarya glyptosperma* type (7.6-20), *Gloeocapsa* (6.1-8), Hystrichospheres (5.1-23; 7.6-20), *Micrasterias* (6.1-4), *Mougeotia* (7.6-31), *M. laetevirens* type (7.6-20), *Pediastrum* (4.1-32, 33; 6.1-2, 4; 7.6-6, 13, 21, 22, 25), *P. boryanum* type (7.6-20, 24), *P. duplex* type (7.6-20, 24), *P. integrum* (7.6-8), *P. patagonicum* (7.6-8), *Pseudoschizaea* (7.6-31), *Scenedesmus* (7.6-22), *Spirogyra* (4.1-29, 32; 7.6-20), *Staurastrum* (6.1-4), *Tetraedron* (7.6-22), *Zygnema* (4.1-29, 32; 7.6-20), Zygnemataceae (7.6-25, 31).

Bryophyta

Musci: *Bartramia*? (7.6-20), *Breutelia*? (7.6-20), *Bryum*? (7.6-20), *Dicranella*? (7.6-20), *Didymon* (7.6-1), *Drepanocladus*? (7.6-20), cf. *Leskea* (7.6-20), *Meesia* (7.6-20), *Rhodobryum*? (7.6-20), *Sphagnum* (7.6-2, 3, 7, 12, 17, 20, 32, 33), *Weissia* (7.6-20). Anthocerotae: *Anthoceros* (7.6-20). Hepaticae: *Phaeoceros* (7.6-20), *P. levis* (7.6-32, 33), *Riccia* (7.6-20).

Ferns and allied groups

Acrostichum (6.1-18, 23; 7.6-20), *A. aureum* (5.1-23), *Adiantum* (7.6-20), *Alsophila* (7.6-23), *A.* cf. *elegans* (7.6-32), *Anemia* (5.1-23; 7.6-20, 32), *Anthyrium dombeyi* type (7.6-20), *Asplenium* (4.1-32; 7.6-20), *A. serra* type (7.6-20), *Azolla* (7.6-20), *A. filiculoides* (7.6-10, 19), *A. microphylla* (7.6-20), *Blechnum* (5.1-23; 6.1-16), *B. imperiale* type (7.6-33), *B. serrulatum* (5.1-23), *B.* (*Salpichlaena*) *volubilis* (7.6-20), *Botrychium* (7.6-12, 20), *B. dusenii* (7.6-3), *Campyloneuron/Polypodium* (7.6-17), cf. *Cheilanthes* (7.6-20, 23),

Cnemidaria–Hemitelia (7.6-23; see also *Hemitelia*), *Crassoretitriletes vanraadshooveni* (7.6-20), *Ctenitis* (7.6-20), *C. pleiosorus* (7.6-18), *C. sloanei* (7.6-18), *C. subincisa* type (7.6-20), *Cyathea* (7.6-13, 18, 20, 21, 23, 30, 32), *C.* (*Alsophila–Sphaeropteris*; 7.6-20), *C.* (*Nephelea*) *cuspidata* type (7.6-20), *C. escuquensis* type (7.6-20), *C. frigida* type (7.6-20), *C. horrida* type (7.6-20), *C.* cf. *schanschin* (7.6-32), *C.* (*Sphaeropteris*; 7.6-20), *C.* (*Trichipteris*; 7.6-20), Cyatheaceae (6.1-16, 19; 7.6-17, 20), *Cystopteris diaphana* type (7.6-20), *C. hypolepis* (7.6-20), *Danaea* type (6.1-18), *Dennstaedtia* (7.6-20), *Dicksonia* (7.6-23, 33), *D. sellowiana* type (7.6-20, 32), *Dryopteris* (4.1-39/40; 6.1-11; 7.6-17), *Elaphoglossum–Asplenium–Hemidictyum* (7.6-17, 20), *E. cuspidatum* (7.6-20), *Eriosorus flexuosus* (7.6-20), fern spores (undifferentiated; 4.1-29), *Grammitis* (6.1-16; 7.6-17, 20, 23), *G.* (*Ctenopteris*) *moniliforme* type (7.6-20), *Gymnogramma* (7.6-32), *Hemitelia* (6.1-18; see also *Cnemidaria*), *Histiopteris incisa* (7.6-20), *Huperzia* (7.6-17), *H.* (*Lycopodium*) *fuegiana* (7.6-12), *H.* (*Lycopodium*) *selago* (7.6-9), Hymenophyllaceae (7.6-12), *Hymenophyllum* (4.1-38; 6.1-16; 7.6-32), *H. myriocarpum* (7.6-20), *H. trichopyllum* (7.6-20), *Hypolepis hostilis* type (7.6-20), *Isoetes* (4.1-32, 36; 6.1-15, 16; 7.6-12, 13, 15, 17, 21–23, 32, 33), *I. boyacensis* (7.6-20), *I. salvatieri* (7.6-12), *Jamesonia* (6.1-16; 7.6-15, 17, 20), *Lindsaea* (7.6-23), *Lophosoria* (6.1-16; 7.6-23), *L. quadripinnata* (7.6-12, 20, 32), *Lycopodium* (6.1-15, 16, 18; 7.6-7, 13, 17, 20, 21, 23), *L. alopecuroides* (7.6-32), *L. cernuum* (7.6-18, 20, 31), *L.* cf. *clavatum* (7.6-18, 32), *L. cuatrecasasii* (7.6-20), *L. curvatum* type (7.6-20), *L. foveolate* (form species; 7.6-20–23, 32), *L. jussiaei* type (7.6-20), *L. magellanicum* (7.6-2), *L. passerinoides* (7.6-18), *L. trianae* (7.6-31), *Lygodium* (5.1-23), *Marattia* cf. *verschaffeltiana* (7.6-32), *Nephrolepis* (7.6-18), cf. *Onychium* (7.6-20), *Ophioglossum* (6.1-16), *O. crotalophoroides* (7.6-20), *O. engelmannii* type (7.6-20), *Osmunda* (7.6-32), *O.* type (6.1-11), *Paesia viscosa* (7.6-20), *Pilularia* (7.6-20), *Pityrogramma* (7.6-18, 20, 21, 23), *P.–Pteris altissima* type (7.6-20), *Pleopeltis* (*Microgramma*) *ciliata* (7.6-20), Polypodiaceae (–Blechnaceae–Pteridaceae) (6.1-19; 7.6-7, 18), *Polypodium* (4.1-32; 5.1-23; 7.6-20, 22, 23), *P. adnatum* (7.6-20), *P. aureum* (7.6-18, 20), *P. feullei* (7.6-12), *Pteridium* (4.1-36; 6.1-11; 7.6-17), *Pteris* (5.1-23; 7.6-21, 23, 31, 32), *P. grandifolia* type (7.6-20), *Saccoloma domingensis* type (7.6-20), *S. elegans* type (7.6-20), cf. *Schizaea* (7.6-20), *Selaginella* (4.1-32, 34; 5.1-23; 6.1-18, 23; 7.6-20, 23), *S. anceps* type (7.6-20), *S.* cf. *excurens* (7.6-32), *S. sellowii* (7.6-20), *Thelypteris* (7.6-20), *T. pilosula* (7.6-18), *Trichomanes* (6.1-20a), tipo trilete (5.1-23).

Gymnosperms

Abies (4.1-29–34, 36, 38), *Araucaria angustifolia* (7.6-33), Cupressaceae (4.1-30; 6.1-11; 7.6-7, 32), *Cupressus–Juniperus* (4.1-32–34, 36, 37, 39/40), *Ephedra* (4.1-30; 6.1-11; 7.6-4–8, 11–13, 17), *E. frustillata* (7.6-2), *E. nevadensis* (4.1-28, 29), *E. trifuca* type (4.1-29), *Juniperus* (4.1-29; 5.1-21; 6.1-1), *J. californica* (4.1-28), *Lepidothamnus* (*Dacrydium*) *fonckii* (7.6-2, 9), *Picea* (4.1-30–33), *Pilgerodendron* (*Libocedrus*) type (7.6-9, 12), *Pinus* (4.1-29–40; 5.1-24; 6.1-1–3, 5–8, 11–14, 17; 7.6-32, 33), *P. caribaea* (5.1-21–23), *P. edulis–P. remota* (4.1-28), *P. tropicalis* (5.1-23), Podocarpaceae (7.6-15, 17, 18), *Podocarpus* (4.1-32; 6.1-2, 3, 5, 6, 11, 13–18; 7.6-7, 8, 21–25, 28, 29, 31–33), *P. angustifolius* (5.1-23), *P. nubigena* (7.6-2, 9, 12), *Saxegothaea* (7.6-7), *S. conspicua* (7.6-9, 12), *Taxodium* (4.1-31), *Tsuga* (4.1-32).

Angiosperms

Acacia (6.1-3, 12, 17; 7.6-7, 25, 30), *A. greggii* (4.1-28; 6.1-3, 12, 17), *Acaena/Polylepis* (7.6-2, 8, 12, 13, 15, 17, 20–23), *Acalypha* (4.1-29, 39/40; 6.1-1, 2, 9–11, 17, 18, 21, 22; 7.6-13–15, 17, 18, 20, 24, 30, 32), Acanthaceae (*Stendandrium*; 7.6-30), *Acantholippia deserticola* (7.6-11), *Acaulimalva* (7.6-20), *Acer* (6.1-11), *Achras* (6.1-3), *Acnistus* (7.6-18), *Acoelorraphe wrightii* (5.1-23), *Acrocomia* (5.1-23), *Adesmia* (7.6-2, 8, 11), *A. ataca-mensis* (7.6-11), *Aeschynomene* (7.6-31), *Aextoxicon* (7.6-12), *Agave* (4.1-29, 30; 6.1-11), *A. deserti* (4.1-28), *A. subsimplex* (4.1-28), *Alchornea* (5.1-24; 6.1-2, 5, 6, 11, 14, 16–18, 22; 7.6-13–17, 20, 21, 28–30, 32, 33), *Alestomeria* [?] (7.6-32), *Alfaroa–Oreomunnea* (4.1-32, 38, 39/40; 6.1-15), Alismataceae (7.6-7), Alismataceae (cf. *Sagittaria*; 7.6-13), *Allionia incarnata* (4.1-28, 29), *Allium* type (6.1-11), *Allophylus* (5.1-23; 7.6-32), *Alnus* (4.1-31–39/40; 6.1-2, 3, 5, 6, 11, 13–18; 7.6-7, 8, 13–18, 21–23, 33), *A. jorullensis* (7.6-20), *Alternanthera* (6.1-1, 11, 19, 20; 7.6-6, 8, 18, 20, 24, 25, 30, 31), Amaranthaceae (cf. *Gomphrena*; 7.6-13), *Amaranthus* (4.1-28; 5.1-23; 7.6-8, 20), *A. australis* (7.6-25), *A. dubius* (7.6-25), *Ambrosia* (4.1-29, 32, 36, 37, 39/40; 5.1-23, 24; 6.1-1–3, 11; 7.6-15, 17, 18, 24, 32), *A. artemisioides* (7.6-11), *A. chenopodiifolia* (4.1-28), *A. deltoidea* (4.1-28), *A. dumosa* (4.1-28), *Amsinckia tessellata* (4.1-28), Anacardiaceae (4.1-33, 34, 39/40; 5.1-23; 6.1-2, 9, 11, 18; 7.6-13, 25, 30), *Anacardium–Tapirira* (7.6-30), *Ananas* (7.6-31), *Anarthrophyllum* (7.6-4, 8), *Anatherostipa venusta* (7.6-11), *Andira* type (7.6-31), Annonaceae (6.1-17, 18), *Antidaphne* (6.1-16), *Antonia* (7.6-31), *Apeiba* (6.1-18), *Aphelandra* (6.1-18), *Apium* type (7.6-8, 32), Apocynaceae (6.1-18; 7.6-13, 20, 25, 30), Araceae (7.6-32), *Aragoa* (7.6-20), Araliaceae (6.1-6, 13, 14; 7.6-25), *Arbutus* (4.1-27), *Arceuthobium* (4.1-32–34, 36), *Arctostaphylos* (4.1-29), *Arenaria* type (7.6-8, 20), cf. *Argemone* (4.1-33), *Argythamnia* cf. *lanceolata* (4.1-28), *A.* cf. *neomexicana* (4.1-28), *A. serrata* (4.1-28), *Aristida adscensionis* (4.1-28; 7.6-11), *Aristolochia* (7.6-31), *Armeria maritima* (7.6-12), *Arrabidaea* (7.6-30), *Artemisia* (4.1-29, 30, 32, 34, 36; 7.6-8, 20), Asclepidaceae (7.6-20), *Astelia pumila* (7.6-3, 12), Asteraceae–Compositae (4.1-30–39/40; 5.1-24; 6.1-1–3, 6, 9–20a, 22; 7.6-5, 6, 9, 13, 15, 17, 18, 20–23, 25, 30–32; Liguliflorae 4.1-29; 7.6-2, 7, 12, 20, 32; Tubuliflorae 6.1-11, 19; 7.6-2–4, 7, 12, 16, 20, 24, 29, 32; low-spine, high-spine, 4.1-29), Compositae: *Ambrosia–Xanthium* (7.6-6), Compositae (Chichorioideae; 7.6-4, 6), Compositae: *Carduus* type (7.6-6), Compositae (Mutisieae; 7.6-4), *Astralagus nuttalianus* (4.1-28), *Astronium* (7.6-20, 30), *Atriplex imbricata* (7.6-11), *Avicennia* (6.1-18), *A. nitida* (7.6-26), *Ayenia* (7.6-20), *Azorella* (7.6-4, 8, 20), *Baccharis* (7.6-32, 33), *B. boliviensis* (7.6-11), *B. tola* (7.6-11), *B.* type (7.6-8), *Banara–Xylosma* (7.6-32), *Barneoudia* (7.6-12), *Bauhinia emarginata* (6.1-18), *Bebbia juncea* (4.1-28), *Begonia* (7.6-14, 32), *Beleperone* (7.6-20), *Berberis* (7.6-2, 4, 7, 12), *Bidens* aff. *pilosa* (7.6-11), *B.* aff. *pseudocosmos* (7.6-11), Bignoniaceae (4.1-37; 7.6-30), *Bocconia* (6.1-11, 16; 7.6-14), *B. integrifolia* (7.6-20), *Boerhavia wrightii* (4.1-28), *Bomarea* (7.6-20), Bombacaceae (4.1-34; 6.1-2, 11, 12, 17; 7.6-25), tipo *Bombax*

(5.1-23; 6.1-3), *Bonamia* (7.6-32), Boraginaceae (4.1-33; 7.6-20), *Borreria* (5.1-23; 6.1-11, 18; 7.6-18, 29, 30, 32), *B. anthospermoides* (7.6-20), *B. laevis* (7.6-20), *B.* cf. *latifolia* (7.6-32), *Bouteloua aristidoides* (4.1-28), *B. barbata* (4.1-28), *B. simplex* (7.6-11), *Bravaisia* (4.1-39/40; 7.6-25), *Brickellia atractyloides* (4.1-28), *B. coulteri* (4.1-28), *Bromelia* (7.6-30), Bromeliaceae (5.1-23; 7.6-30), *Bromus catharicus* (7.6-11), *Brosimum* (4.1-39/40; 6.1-1, 9–11), *Brugmansia* (*Datura–Methysticodendron*; 7.6-20), *Bucida/Conocarpus* (5.1-23), *Buddle(j)ia cordata* (4.1-27), *Buettneria* (6.1-18), *Bunchosia* (5.1-23), *Bursera* (4.1-29, 32, 33, 37, 39/40; 5.1-24; 6.1-1, 3, 5, 6, 9–14, 18, 20; 7.6-24, 25), *B. microphylla* (4.1-28), *B. simaruba* (5.1-23), Burseraceae (6.1-2, 8), *Byrsonima* (4.1-39/40; 6.1-1, 2, 9, 11, 18–20; 7.6-25, 29, 30), *B. crassifolia* (6.1-17), *Cabralea* (7.6-31), Cactaceae (4.1-39/40), Cactaceae (cf. *Cereus*; 7.6-17, 30), *Caesalpinia* (5.1-24), *Calandrinia* (7.6-8, 20), *Calceolaria* (7.6-20), *Calliandra* (6.1-17, 18; 7.6-31, 32), *Calophyllum* (5.1-22), *Caltha* (7.6-3, 9, 12), *Calycera* (7.6-6), *Camissonia claviformis* (4.1-28), Campanulaceae (cf. *Rhizocephalum*; 7.6-13), *Campnosperma* (6.1-23), *Canavalia* (6.1-18), *Caperonia palustris* (5.1-23), Caprifoliaceae (4.1-30, 37), cf. *Cardiospermum* (7.6-20), *Carnegiea gigantea* (4.1-28), *Carpinus–Corylus–Ostrya* (4.1-31–34, 36; 6.1-2, 3), *Carya* (4.1-32, 33, 37), *Caryocar* (7.6-30), Caryophyllaceae (4.1-29, 33, 37, 39/40; 6.1-3, 9, 11, 16, 20; 7.6-2–4, 7, 9, 12, 13, 15, 20–23, 31, 32), *Casearia* (5.1-23), *Cassia* (7.6-20, 30–32), *Cassipourea* (6.1-18), *Castela* type (7.6-25), *Catopsis* (6.1-18), *Catostemma* (?) (5.1-23), *Cavanillesia* (6.1-18; 7.6-30), *Cecropia* (4.1-39/40; 5.1-24; 6.1-1, 2, 9, 11, 16, 19–22; 7.6-14, 16, 20, 21, 24, 25, 28–30, 32), *Cedrela* (7.6-20, 30), *C.* cf. *fissilis* (7.6-32), *Ceiba* (6.1-11, 13, 14, 18), Celastraceae type (6.1-11), *Celtis* (4.1-30, 33, 37, 39/40; 5.1-24; 6.1-1–3, 6, 9–14, 17; 7.6-7, 14, 20, 24, 29–33), *Ceratophyllum* (4.1-36), *Ceratosanthes* (7.6-31), *Cercidium floribundum* (4.1-28), *C. floridum* (4.1-28), *C. microphyllum* (4.1-28), *Cercophora* type (7.6-8), *Cereus* (7.6-7, 30), *Chaenactis* cf. *stevioides* (4.1-28), *Chaetoptelea* (4.1-39/40; 6.1-3, 5, 6, 9, 13, 14), *Chamaesyce* (7.6-30), chenoam (4.1-29–39/40; 5.1-23, 24; 6.1-1–3, 6, 7, 9–14, 17–19, 22; 7.6-2–8, 12, 13, 15, 17, 20, 24, 32), *Chlorophora* (4.1-39/40; 6.1-1; 7.6-25), *Chorisia* (7.6-31), *Chorizanthe brevicornu* (4.1-28), *C. commisuralis* (7.6-11), *C. corrugata* (4.1-28), Chrysobalanaceae (6.1-20a), *Chrysobalanus icaco* (5.1-21, 22), *Chrysophyllum* (7.6-32), *C. marginatum* (7.6-32), *Chrysothamnus teretifolius* (4.1-28), *Chuquiraga atacamensis* (7.6-11), *Chusquea* (6.1-20a), *Cirsium* (4.1-29), *Cissus* (5.1-23; 6.1-18), *C. striata* (7.6-12), 7.6-12), *Cistanthe* (7.6-11), *Citrus* type (6.1-3), *Cladium* (5.1-24), *C. jamaicense* (5.1-23), *Clarisia* (7.6-25), *Cleome* (6.1-16; 7.6-20), *Clethra* (6.1-16; 7.6-13, 14, 20, 32, 33), *Clusia* (6.1-16; 7.6-20), *C. criuva* (7.6-32), *C. fossilia* (7.6-26), Clusiaceae (7.6-13), Clusiaceae/*Calophyllum* (7.6-30), *Cnidoscolus* (7.6-30), *Coccoloba* (6.1-3, 11, 12, 18), *Coccothrinax* (5.1-22), *Colpothrinax wrightii* (5.1-23), Combretaceae–Melastomataceae (6.1-11), *Combretum–Terminalia* (6.1-3, 8, 12, 18; 7.6-30, 31), Compositae (see Asteraceae–Compositae), *Compsoneura* (6.1-18), *Conocarpus* (5.1-21; 6.1-18), *C. erectus* (7.6-26), *Condalia* (7.6-7), cf. *Conomorpha* (7.6-20), Convolvulaceae (4.1-37; 7.6-7), cf. *Conyza deserticola* (7.6-11), *Copaifera* (6.1-18; 7.6-30, 31), *Corchorus* (5.1-23; 6.1-11), *Cordia* (4.1-39/40), *C. alliodora* (6.1-18), *C. curassavica* (7.6-30), *C. galeottiana* (5.1-22), *C. lantana* (7.6-20, 30), *C. sebestena* (5.1-22), *Coriaria ruscifolia* (7.6-20), *Couroupita* (6.1-18), *Cristaria* (7.6-11), *Crotalaria* (7.6-8, 30), *Croton* (7.6-18, 20, 32), *C. bogotense* type (7.6-20), Cruciferae–Brassicaceae (4.1-29, 33; 6.1-11, 16; 7.6-4, 6–8, 13), *Crotalaria* (7.6-8), *Cryptantha barbigera* (4.1-28), *C. decipiens* (4.1-28), *C. diffusa* (7.6-11), *C. hispida* (7.6-11), *C. limensis* (7.6-11), *C. maritima* (4.1-28), *C. phaceloides* (7.6-11), *C. pterocarya* (4.1-28), Cucurbitaceae (7.6-25), Cunoniaceae (7.6-31), *Cupania* (6.1-18), *Cuphea* (4.1-33; 5.1-23; 7.6-20, 30, 31), *C.* cf. *ingrata* (7.6-32), *C.* cf. *urbaniana* (7.6-32), Cupuliferoidae (Fagales, fagaceous; 6.1-8), *Curatella* (7.6-30, 31), cf. *Cydista* (7.6-20), Cyperaceae (4.1-29–33, 35, 36, 38, 39/40; 5.1-23, 24; 6.1-1–3, 6, 8, 10, 11–23; 7.6-2–4, 6–8, 12, 13, 15–18, 20–25, 29, 31–33), *Cyperus* (5.1-23; *Cyperus–Kyllinga* 6.1-20a), *Cyrilla* (6.1-23), *C. racemiflora* (5.1-23), *Dalbergia* (4.1-39/40), *Dalea* (7.6-20), *D. mollis* (4.1-28), *D. mollissima* (4.1-28), *Dalechampia* (7.6-20), *Daphnopsis* (5.1-23; 7.6-20), *D.* cf. *beta* (7.6-32), *Daucus* type (7.6-6), *Desfontainia spinosa* (7.6-12), *Dialyanthera* (6.1-18), *Dicliptera* (7.6-20), *Dicoria canescens* (4.1-28), *Dictyocaryum* (7.6-14), *Didymopanax* (7.6-24, 29, 31, 32), *Dioclea* (7.6-30), *Diplostephium meyenii* (7.6-11), *Ditaxis lanceolata* (4.1-28), *Dodonaea* (4.1-33, 34; 7.6-8, 15, 17, 23), *D. arborea* (6.1-11), *D. viscosa* (7.6-20), *Donatia* (*Avicennia*) *fascicularis* (7.6-3, 12), *Draba* (7.6-20), *D. cuneifolia* (4.1-28), *D. hammenii* (7.6-20), *Drapetes muscosus* (7.6-9, 12), *Drepanocarpus* type (6.1-18), *Drimys* (6.1-15, 16), *D. brasiliensis* (7.6-20), *D. granadensis* (7.6-20), *D. winteri* (7.6-2, 3, 9, 12), *Drosera* (7.6-30, 31), *Drymaria villosa* type (7.6-20), *Dyckia* (7.6-31), *Eccremocarpus longiflorus* (7.6-20), *Echervia* (7.6-20), *Echinocereus* (4.1-28; 6.1-11), *Echinodorus* (7.6-32, 33), *Echinopsis atacamensis* (7.6-11), *Eichornia* (4.1-39/40; 7.6-33), *E. crassipes* (5.1-23), *Embothrium coccineum* (7.6-2, 9, 12), *Emmotum* (7.6-31), *Empetrum* (7.6-4, 7, 12), *E.*–Ericaceae (7.6-3, 9, 12), *E. rubrum* (7.6-2, 12), *Encelia* type (7.6-8), *E. farinosa* (4.1-28), *Epilobium* (7.6-20, 23), Ericaceae (4.1-33, 34; 5.1-23; 6.1-15–18; 7.6-12–17, 20, 21, 23, 30–32), Eriocaulaceae (6.1-16), *Eriocaulon* (7.6-30), *E.–Paepalanthus* (7.6-32, 33), *Eriogonum* (4.1-30), *E. fasciculatum* (4.1-28), *E. wrightii* (4.1-28), *Erioneuron pulchellum* (4.1-28), cf. *Eriosema* (7.6-20), *Eriotheca* (7.6-31), *Eryngium* (4.1-29, 34, 37; 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7.6-31), *Porophyllum gracile* (4.1-28), Portulacaceae (4.1-29; 6.1-18; 7.6-23), *Potamogeton* (4.1-29, 32, 33, 36, 39/40; 5.1-24; 6.1-3; 7.6-15, 31), *Pouteria* (7.6-30), Primulaceae (7.6-7), *Prosopis* (4.1-30; 7.6-4, 7), *P. velutina* (4.1-28), Proteaceae (4.1-39/40; 6.1-11; 7.6-16, 20, 23, 31), *Protium* (6.1-23; 7.6-25, 30), *P. cubense* (5.1-23), *Prunus* type (7.6-32), *Pseudobombax* (6.1-18), *Pseudopanax laetevirens* (7.6-9, 12), *Psychotria* (7.6-32), *P.* cf. *alba* (7.6-32), *Pterocarpus officinalis* type (6.1-18), *Pterocarpus–Sclerolobium* (7.6-30), *Puya* (6.1-16; 7.6-17, 20), *Quararibea* (6.1-18), *Quassia* (6.1-18), *Quercus* (4.1-29–39/40; 6.1-1–3, 5–8, 11–14, 16, 17, 19, 20; 7.6-20), *Q. hahnii* (4.1-27), *Q. hartwegi* (4.1-27), *Q. laeta* (4.1-27), *Q. laurina* (4.1-27), *Q. repanda* (4.1-27), *Q. rugosa* (4.1-27), *Q. rugulosa* (4.1-27), *Quinchamalium* (7.6-12), *Rafinesquia neomexicana* (4.1-28), *Randia* (6.1-18), Ranunculaceae (4.1-29, 33; 7.6-2, 6, 7, 12, 13), *Ranunculus* (6.1-16; 7.6-8, 20), R. cf. *bonariensis* (7.6-32), *Rapanea* (7.6-20, 21, 24, 25, 30–32), *Raphia* (6.1-23), *Rauwolfia* (5.1-23; 6.1-18), *Relbunium* (7.6-20, 32), *Rhamnus* type (7.6-32), *Rhaphithamnus spinosus* (7.6-12), *Rhizocephalum* (7.6-23), *R. candollei* (7.6-20), *Rhizophora* (4.1-38, 39/40; 6.1-18; 7.6-28), *R. mangle* (5.1-23; 7.6-26), *Rhus* (4.1-29; 7.6-20), *Ribes* (4.1-27, 37; 7.6-2, 7, 12), *R. magellanicum* (7.6-3), Rosaceae (4.1-29, 30, 33; 6.1-11, 16; 7.6-4, 7, 20), *Roupala* (7.6-31, 32), Rubiaceae (4.1-29, 37; 6.1-2, 16–18; 7.6-2, 4, 6, 7, 12, 20, 30, 32), Rubiaceae (cf. *Borreria*; 7.6-13), *Rumex* (6.1-2, 11; 7.6-2, 4, 7, 15, 21), *R. tolimensis* (7.6-20), *Ruppia maritima* (4.1-32; 7.6-8, 24), Rutaceae (6.1-11; 7.6-30), Rutaceae/*Esenbeckia* (7.6-30), *Sabal parviflora* (5.1-23), *Sagittaria* (4.1-32), *S.–Echinodorus* (7.6-20, 30), *Salacia* (7.6-31), Salicaceae (7.6-7), *Salix* (4.1-31, 32, 34, 36, 37; 6.1-11), *Salpichroa* type (7.6-8), *Salvia killipiana* type (7.6-20), *S. polystachia* (4.1-27), *S.* type (7.6-30), Sapindaceae (6.1-2, 11, 21; 7.6-30), *Sapindus* (5.1-24), *Sapium* (6.1-2, 14, 16, 18; 7.6-20, 30), Sapotaceae (4.1-39/40; 5.1-23, 24; 6.1-3, 5, 6, 12, 14, 17, 19), *Sarcobatus* (4.1-29, 30), *Satureja* (4.1-37), *S. nubigena* type (7.6-20), *Schinus* (7.6-4, 6, 7), *Schkuhria multiflora* (7.6-11), *Scirpus* (7.6-17), *Sclerolobium* (see *Pterocarpus–Sclerolobium*), Scrophulariaceae (4.1-37; 7.6-7), *Scybalium* (7.6-20), *Sebastiania* (7.6-30), *Sebastinia brasiliensis* (7.6-32), *S. commersoniana* (7.6-32), *S.* cf. *schottiana* (7.6-32), *Sebastiania* type (6.1-11), *Sechium* (6.1-18), *Senecio* (4.1-27; 6.1-12; 7.6-8, 32, 33), *S.* aff. *atacamensis* (7.6-11), *Sericotheca argentea* (7.6-20), *Serjania* (7.6-30, 32), *Sessea* (7.6-20), *Sida* (7.6-25), *Simarouba* (7.6-30), *Simmondsia chinensis* (4.1-28), *Sisyrinchium* (7.6-20), *Sisymbrium philippianum* (7.6-11), *Smilax* (7.6-31), Solanaceae (4.1-30, 33; 5.1-24; 6.1-2, 11, 16, 17; 7.6-4, 6–8, 13, 20, 30, 31), *Solanum* (6.1-3, 6, 12; 7.6-8, 32), *S. hindsianum* (4.1-28), *Sparganium* type (6.1-11), *Spegularia* (7.6-11), *S.* type (7.6-6), *Sphaeralcea* (4.1-28), *Spondias* (5.1-23; 6.1-2, 3, 12; 7.6-24, 25), *S. lutea* (5.1-21, 22), *Stegnosperma halimifolium* (4.1-28), *Stendandrum* (see Acanthaceae), *Stipa chrysophylla* (7.6-11), *S. speciosa* (4.1-28), *Struthanthus* (7.6-32), *Stryphnodendron* (7.6-30, 31), *Styloceras laurifolium* (7.6-20), *Styrax* (7.6-31, 32), *S. rosadoi* (7.6-27), *Swartzia panamensis* type (6.1-18), *Symphonia* (6.1-18; 7.6-16, 30), *Symphoricarpos microphyllus* (4.1-27), *Symplocos* (6.1-16, 18; 7.6-20, 31), *S. lanceolata* type (7.6-32), *S. tenuifolia* type (7.6-32), *Tabebuia* (7.6-30), *Tabernaemontana* (6.1-18), *Tagetes multiflora* (7.6-11), *Tapirira* (7.6-25, 32; see also *Anacardium–Tapirira*), *Tarasa operculata* (7.6-11), *T.* type (7.6-8), *Tepualia stipularia* (7.6-12), *Terminalia* (see *Combretum–Terminalia*), *Tetroncium magellanicum* (7.6-2, 3), *Tetrorchidium rubrivenium* (7.6-32), *Thalictrum* (4.1-29, 32–34, 36; 6.1-16; 7.6-8, 17), *T. podocarpum* (7.6-20), *Thrinax radiata* (5.1-22), *Tidestromia* (4.1-30), *Tilia* (4.1-36), Tiliaceae (6.1-11; 7.6-16, 20), *Tiquilia atacamensis* (7.6-11), *Tournefortia* (7.6-20), *Trechonaetes* (7.6-8), *Trema* (4.1-39/40; 5.1-23, 24; 6.1-1, 3, 5, 6, 10–12, 14, 20–22; 7.6-14, 24, 25, 32; *T. floridana* 6.1-12), *Tribulus* (5.1-23; 7.6-25), *Trichanthera* (6.1-18), *Trichilia* (7.6-30–32), *Trifolium* type (7.6-8), *Trigonia* (7.6-32), *Tristerix* (7.6-12, 20, 32), *T. longebracteatus* type (7.6-20), *Tristicha* (6.1-18), *Trixis* (7.6-32), *T. californica* (4.1-28), *Trophis* (4.1-39/40; 6.1-10), *Typha* (4.1-29–32, 35, 36, 39/40; 5.1-23, 24; 6.1-1–3, 8, 18, 19, 21; 76.-6, 7, 20, 25, 31), *T. angustifolia* (7.6-8, 24), *T. domingensis* (5.1-23; 7.6-32), Ulmaceae (6.1-3; 7.6-20), Ulmaceae (cf. *Trema–Lozanella*; 7.6-15), *Ulmus* (4.1-32, 33, 39/40; 6.1-11, 16), Umbelliferae (4.1-30, 32, 33, 37; 5.1-23; 6.1-15–17, 21; 7.6-2, 3, 6–9, 12, 13, 15, 17, 20, 21, 23, 30–33), *Urmenetea atacamensis* (7.6-11), Urticaceae–Moraceae (4.1-29, 33, 34; 6.1-11, 20–22; 7.6-6–8, 30, 32), Urticales (4.1-39/40; 6.1-1, 16, 18; 7.6-15, 17, 22, 23), *Urvillea* (7.6-20, 32), *Utricularia* (4.1-33; 5.1-23; 7.6-20, 32), *Valeriana* (4.1-33; 6.1-16; 7.6-2, 9, 12, 13, 15, 17, 20, 21, 23), *V. arborea* type (7.6-20), *V. stenophylla* type (7.6-20), *V. triphylla* type (7.6-20), Valerianaceae (7.6-32), *Vallea* (7.6-13, 14, 20), *Vellozia* (7.6-30, 31), *Verbena* (4.1-28; 7.6-32), Verbenaceae (7.6-4, 6, 8), *Veronia* (7.6-32), *Viburnum* (6.1-16; 7.6-20), *Vicia* (7.6-20), *Viguiera* cf. *deltoidea* (4.1-28), *V. laciniata* (4.1-28), *Villaresia* (7.6-31), *Viola* (7.6-20), *Virola* (6.1-18), *Vismia* (7.6-20), Vitaceae (6.1-11), *Vitis* (6.1-3), *Vochysia* (6.1-18), *Vulpia* (4.1-28), *Warszewiczia* (7.6-20), *Weinmannia* (6.1-11, 16; 7.6-15, 16, 20, 23, 32, 33), *W. trichosperma* (7.6-9, 12, 13, 17), *Xylopia aromatica* (5.1-23; see also *Banara–Xylosma*), *Xyris* (7.6-32, 33), *Zanthoxylum* (6.1-3, 17; 7.6-18, 30, 32), *Z. panamensis* (?; 6.1-18), *Z. setulosum* (6.1-18), *Zea–Z. mays* (4.1-31, 33, 34, 36, 37, 39/40; 5.1-24; 6.1-1–3, 6, 8–13, 18, 21, 22; 7.6-15, 32), *Zizyphus* (7.6-30), *Zuelania* (6.1-3).

APPENDIX 2.2

Late Cretaceous and Cenozoic plants mentioned in the text, arranged by plant group/family. Numbers in parentheses refer to references and other information given in Tables 4.1 (Mexico), 5.1 (the Antilles), 6.1. (Central America), 7.1 (South America, Late Cretaceous and Paleogene), 7.2 (South America, Neogene), 7.6 (South America, Quaternary). For references cited in the Appendix see References in Chapters 4–7. The classification of ferns at the family level is currently under revision, and they are arranged here alphabetically by genus, as at MO; for provisional family assignments see Tryon and Tryon (1982; reference Chapter 3). Multiple listings for a single taxon may include some aff., cf., and ? designations by the original authors. Some pollen species are listed under a family and under Other Angiosperms depending on the designations of the original author(s), and both sections should be checked when searching for the fossil occurrence of a taxon. Age ranges (fide original authors; updated in Table 7.3 for South America) are indicated by K (Cretaceous), Pa (Paleocene), E (Eocene), O (Oligocene), M (Miocene), Pl (Pliocene), and Q (Quaternary). For additional suggested affinities and stratigraphic ranges, see Germeraad et al. (1968), Muller (1981), Taylor (1990), Collinson et al. (1993), and Holmes (1991; these references in Chapter 7).

Bacteria

Bacillus (5.1-19 M).

Fungi

Ascomycete cleistothecium (6.1-9 M), *Ascomycetes* (7.1-83 Pa), *Asteria* (7.6-20 Q), *Asterinites colombiensis* (7.1-83 Pa), *A. tellezii* (7.1-83 Pa), *Athelia* (7.6-20 Q), *Brefeldiellites argentina* (7.1-4 K), *Caenomyces braziliensis* (7.2-46 Pl), *Callimothallus corralescence* (7.1-79 K), *Circulisporites* (7.2-45 M), *Coprinites dominicana* (5.1-11 M), *Dicellaesporites* (7.1-31, 32, 34, 35 Pa, 59, 61 E, 64 E–O), *D. fusiformis* (7.1-83 Pa), *D. magnus* (7.1-83 Pa), *D. rinconii* (7.1-83 Pa), *Didymoporisporonites* (7.1-61 E), *Diporisporites* (7.2-45 M), *D. elongatus* (7.1-34, 35 Pa), *D. hammenii* (7.1-83 Pa), *Dyadosporonites annulatus* (7.1-45 E), *Entomophthora* (5.1-12 M), fungal spores (6.1-2 Q, 8 Q, 16 Q), *Fussiformisporites lineolatus* (7.1-80 K), *F. polyhedricus* (7.1-100 K), *Gaeumannomyces* cf. *caricis* (7.6-20 Q), *Geastrum tepexensis* (4.1-12 O/O–M), *Gelasinosperma adjuncta* (7.6-20 Q), *G. retispora* type (7.6-20 Q), *Geotrichites glaesarius* (5.1-13 M), *Granatisporites* (7.1-59, 61 E, 64 E–O), *Helicoon pluriseptatum* (7.6-20 Q), *Hiospira* (7.2-39 Pl; 7.6-20 Q), *Hysterites ellipticus* (7.2-31 M), *Inapertisporites* (7.1-59, 61 E, 64 E–O), *I. ovalis* (7.1-34, 35 Pa), *Lacrimasporonites* (7.1-45, 59, 61 E, 64 E–O; 7.2-45 M), *L. arcuatus* (7.1-83 Pa), *L. ovalis* (7.1-83 Pa), *Micropeltis* (7.6-20 Q), *Microthyrium* (6.1-13 Pl; 7.2-39 Pl; 7.6-20 Q), *Microthryiacites baqueroensis* (7.1-4 K), *Molinea asterinoides* (7.1-79 K), *Monoporisporites* (7.1-59, 61 E, 64 E–O), *M. grandis* (7.1-80 K), *M. perminutus* (7.1-83 Pa), *Multicellaesporites* (7.1-31, 32 Pa, 59, 61 E, 64 E–O), *M. cerrejonensis* (7.1-83 Pa), *Neurospora* (7.2-39 Pl; 7.6-20 Q), *Pleospora* (7.6-20 Q), *Plochmopeltinites masonii* (7.1-45 E), *Pluricellaesporites* (7.1-34, 35 Pa, 59, 61 E, 64 E–O), *P. psilatus* (7.1-45 E), *Polyadosporites* (7.1-83 Pa), *Sphaerites consociatus* (7.2-31 M), *S. punctiformis* (7.2-31 M), *S. sparsus* (7.2-31 M), *Sphaerodes* (7.6-20 Q), *Spirotremesporites ecuatorialis* (7.6-20 Q), *S. simplex* (7.6-20 Q), cf. *Stemphyllum* (7.6-20 Q), *Tetraploa aristata* (7.2-50 M; 7.6-20 Q), *Tilletia sphagni* (7.6-20 Q), *Trichopeltinites pulcher* (7.1-4 K), *Ulospora* (7.6-20 Q), *Xylomites immersus* (7.2-31 M).

Algae and allied groups

Amphitrema flavum (7.6-20 Q), *Arcella arenaria* (Protista, 7.6-20 Q), *A. brasiliensis* (7.6-20 Q), *A. catinus* (7.6-20 Q), *A. discoides* (7.6-20 Q), *A. polypora* (7.6-20 Q), *Assulina seminulum* (7.6-20 Q), *Botryococcus* (4.1-32 Q; 5.1-23 Q; 6.1-2 Q, 4 Q, 8 Q, 16 Q; 7.1-20 K; 7.2-8, 10, 43, 50 M; 7.6-8, 21, 22, 24, 25, 29, 33 Q), *B. braunii* (7.1-46 E, 49, 52 O, 61 E, 65 K/Pa; 7.6-20 Q), *Canningia minor* (5.1-3 K), *Catinipollis geiseltalensis* (7.1-37 Pa, 47 E), *Chara woodringi* (5.1-16 M), *Chlamydomonas* (7.6-31 Q), *Chomotriletes* (7.1-91 E), *Chondrites dictyotoides* (5.1-8 O), *C. subsimplex* (7.1-58 E; 7.2-19a M), *Coelastrum* (7.6-25 Q), *C. reticulatum* (7.6-20 Q), *Cometodinium whitei* (7.1-74 K), *Confossia rara* (7.1-11 K), *C. vulgaris* (7.1-11 K), *Cossmarium* (7.6-20 Q), *Debarya glyptosperma* type (7.6-20 Q), *Diplotesta inflata* (5.1-3 K), *Gloeocapsa* (6.1-8 Q), *Hystrichosphaera* (5.1-23 Q; 7.6-20 Q), *Hystrichosphaeridium* (5.1-3 K), *H. arundum* (5.1-3 K), *Micrasterias* (6.1-4 Pl; 7.1-91 E), *Mougeotia* (7.1-47 E; 7.2-43 M; 7.6-31 Q), *M.* cf. *laetivirens* (7.1-47 E; 7.6-20 Q), *Operculodinium* (6.1-11 M/M–Pl, 12 Pl; 7.1-91 E), *O. centrocarpus* (6.1-9 M), *Palaeostomocystis fragilis* (5.1-3 K), *Patera crassa* (7.1-11 K; alga?, position unknown), *P. tenuis* (7.1-11 K), *Pediastrum* (4.1-10 E, 32, 33 Q; 6.1-2, 4 Q; 7.1-20 K, 31, 32 Pa, 49, 52, 66 E–O; 7.2-8, 10, 43, 50 M; 7.6-6, 13, 21, 22, 25 Q), *P. boryanum* type (7.6-20, 24 Q), *P.* cf. *duplex* (7.1-50 O; 7.6-20, 24 Q), *P. integrum* (7.6-8 Q), *P. paleogeneites* (7.1-100 K), *P. patagonicum* (7.6-8 Q), *Prismatocystis ewingii* (5.1-3 K), *Pseudoschizaea* (7.6-31 Q), *Pterospermella* (7.1-74 K), Pyrrophyta (6.1-10 M), *Scenedesmus* (7.6-22 Q), *Schizocystia* (7.1-74 K), *Schizosporis reticulatus* (7.1-10 K, plankton), *Scriniodinium* (5.1-3 K), *Spiniferites* (6.1-9 M), *Spirogyra* (4.1-29, 32 Q; 7.1-47 E; 7.2-39 Pl; 7.6-20 Q), *Staurastrum* (6.1-4 Q), *Stephodinium* cf. *europaicum*, *Tasmanites* (7.1-52 O), *Tetraedron* (7.6-22 Q), *Zygnema* (4.1-29, 32 Q; 7.1-47 E; 7.6-20 Q), Zygnemataceae (7.6-25, 31 Q), zygospores of Zygnemataceae (7.1-49 O–M).

Bryophyta

Aequitriradites baculatus (7.1-74 K; see also ferns below), *Anthoceros* (4.1-18 O/O–M; 7.6-20 Q), *Baccania* (see Miocene amber), *Bartramia*? (7.6-20 Q), aff. *Breutelia* (7.2-39 Pl; 7.6-20 Q), *Bryum*? (7.6-20 Q), *Cinguitriletes australis* (7.1-49, 51, 52 O), *Coptospora foveolata* (7.1-5 K), *Dicranella*? (7.6-20 Q), *Didymdoon* (7.6-1 Q), *Drepanocladus*? (7.6-20 Q), *Drepanolejeunia* (Miocene amber), *Frullania* (Miocene amber), aff. Hookeriaceae (7.2-39 Pl), aff. *Lejeunea* (7.2-39 Pl), cf. *Leskea* (7.6-20 Q), *Meesia* (7.6-20 Q),

Muscites (7.2-30 M), *Octoblepharum* (Miocene amber), *Phaeoceros* (6.1-13; 7.6-20 Q), *P. levis* (7.6-32, 33 Q), aff. *Prionolejeunea* (7.2-39 Pl), *Reboulisporites fuegiensis* (7.1-47 E), *Rhodobryum*? (7.6-20 Q), *Riccia* (7.6-20 Q), *Ricciaesporites* (7.2-10 M), *R. transdanubicus* (7.2-13 M), *Sphagnum* (4.1-18 O/O–M; 7.1-59 E; 7.2-39 Pl; 7.6-2, 3, 7, 12, 17, 20, 32, 33 Q), *Taurocusporites segmentatus* (7.1-10 K), aff. Thuidiaceae (7.2-39 Pl), *Triporoletes reticulatus* (7.1-10 K), *Weissia* (7.6-20 Q).

Ferns and allied groups

Achradosporis lurensis (7.1-19 K), *Acrostichum* (6.1-6–9 M, 12, 15 Pl, 18, 23 Q; 7.6-20 Q), *A. aureum* (5.1-23 Q), *A. linearifolium* (7.2-21 M, 23, 25 Pl), *A. mexicanum* (4.1-24 M), *Adianites borgoniana* (7.1-58 E; 7.2-19a M), *Adiantum* (6.1-15 Pl; 7.6-20 Q), *A. patagonicum* (7.1-8 K), *Aequitriradites* (7.1-10, 100 K), *A. baculatus* (7.1-5, 74 K; see also Bryophyta above), *A. spinulosus* (7.1-2, 3, 5 K), *A. verrucosus* (7.1-2, 3, 5 K), *Alsophila* (4.1-26 Pl; 5.1-20 M; 6.1-10 M; 7.6-23 Q), *A.* cf. *elegans* (7.6-32 Q), *Alsophilidites kerguelensis* (7.1-56 Pa), *Alsophilocaulis calveloi* (7.2-1 M), *Anemia* (4.1-23 M; 5.1-23 Q; 7.6-20, 32 Q), *Antrophyum* (5.1-20 M; 6.1-7–9 M, 12, 14 Pl), *Antulsporites baculatus* (7.1-3 K), *Apiculatisporis* [*-rites*] (7.1-37 Pa, 74 K), *A.*(?) *cingulatus* (7.1-85 Pa–E), *A. obscurus* (7.1-85 Pa–E), *Appendicisporites* (4.1-10 E; 7.1-80 K), *A.* cf. *stylosus* (7.1-3 K), *Aratrisporites ocellatus* (7.1-99 K), *Ariadnaesporites micromedusus* (7.1-11 K), *A. spinosus* (7.1-100 K), *Asplenium* (4.1-32 Q; 7.1-15 E; 7.2-16 M; 7.6-20 Q), *A. incertum* (7.1-41 E), *A. serra* type (7.6-20 Q), *Asterisporites chlonovae* (7.1-3 K), *Athyrium dombeyi* type (7.6-20 Q), *Auriculozonospora spongiosa* (7.1-4 K), *Auritulinasporites* (7.1-5, 74 K), *Azolla* (7.1-17, 19, 20 K, 37 Pa, 52 O, 65 K, Pa; 7.2-8, 13 M, 39 Pl, 43 M; 7.6-20 Q), *A. filiculoides* (7.6-10, 19 Q), *A. microphylla* (7.6-20 Q), *A. polyancyra* (7.1-11 K), *Baculatisporites* (7.1-34, 35, 37 Pa, 49 O, 85 Pa–E), *B. comaumensis* (7.1-2, 5 K, 42, 46, 47 E, 56 Pa, 74 K), *B. multibaculae* (7.1-80, 81 K), *B. turbioensis* (7.1-29 Pa, 42, 46 E, 51, 52 O), *Bacutriletes* (7.2-50 M), *B. guttula* (7.1-4 K), *B. triangulatus* (7.1-4 K), *Baqueroites padulae* (7.1-4 K), *Biretisporites* (4.1-11 O/O–M; 7.1-2, 5, 19 K, 29, 37 Pa; 7.2-10 M), *B. crassilabratus* (7.1-42, 46 E, 51, 52 O), *B. potoniaei* (7.1-74, 90, 99 K), *Blechnum* (5.1-23 Q; 6.1-16 Q; 7.1-9 K, 57 E; 7.2-16 M), *B. antediluvianum* (7.1-58 E; 7.2-19a M), *B. betijoquensis* (7.2-40 M), *B. imperiale* type (7.6-33 Q), *B. serrulatum* (5.1-23 Q), *B.* (*Salpichlaena*) *volubilis* (7.6-20 Q), *Botrychium* (7.6-12, 20 Q), *B. dusenii* (7.6-3 Q), *Buttinia andreevi* (7.1-80, 81 K), *Cadispora* (7.1-74 K), *Calamospora* (5.1-3 K), *C. mesozoica* (7.1-5 K, 65 K–Pa), *Callialasporites dampieri* (7.1-90 K), *Camarazonosporites* (4.1-10 E; 7.1-74 K, 85 Pa–E, 99 K), *C. microalveolatus* (7.1-5 K), *Campyloneurum–Polypodium* (7.6-17 Q), *Carbochonicus carbunculus* (7.1-4 K), *Caudaspora spinosa* (7.1-67, 68 K), *C. verrucata* (7.1-67, 68 K), *Ceratopteris* (see Dettmann & Clifford, 1992; 4.1-21 O/O–M, 26 Pl; 6.1-2 E, 8,10 M, 15 Pl–Q), *Ceratosporites* (7.1-10, 99 K), *C. equalis* (7.1-5 K), *C. setosus* (7.1-5 K), cf. *Cheilanthes* (7.6-20, 23 Q), *Chomotriletes fragilis* (7.1-66 E–O), *C. minor* (7.1-5 K [incertae sedis; possibly bryophyte spore fide original author], 74 K, 85 Pa–E), *Cibotiidites* (7.1-74, 80 K), *C. auriculatus* (7.1-5 K), *Cicatricosisporites* (4.1-10 E, 11 O/O–M; 5.1-3 K; 7.1-10, 11 K), *C. annulatus* (7.1-5, 74 K), *C. australiensis* (7.1-2, 3, 5, 10, 74, 90 K), *C. avnimelchi* (7.1-90 K), *C. baculatus* (7.1-100 K; 7.2-43 M), *C. baqueroensis* (7.1-5 K), *C. berouensis* (7.1-74 K), *C. brevilaesuratus* (7.1-99 K), *C. crassiterminatus* (5.1-2 K), *C. cristatus* (7.1-100 K), *C. decussatus* (7.1-85 Pa–E), *C. dorogensis* (7.1-85 Pa–E, 90, 100 K; 7.2-43 M), *C. eocenicus* (7.1-85 Pa–E), *C.* cf. *ethmos* (7.1-5 K), *C. giganteus* (7.1-5 K), *C. hallei* (7.1-74, 99 K), *C. hughesii* (7.1-3, 5, 10 K), *C. mediostriatus* (7.1-99 K), *C. microstriatus* (7.1-99 K), *C. nuni* (7.1-99 K), *C. potamacensis* (7.1-90 K), *C. reticiatricosus* (7.1-90 K), *C. subrotundus* (7.1-74, 90, 99 K), *C. ticoensis* (7.1-5 K), *C. venustus* (7.1-78d, 99, 100 K), *Cingulatisporites* (7.2-43 M), *C. verrucatus* (7.1-90, 100 K), *Cingutriletes australis* (7.1-29 Pa, 42, 46 E, 49 O), *Cladophlebis antarctica* (7.1-4 K), *C. browiana* (7.1-4 K), *C. haiburnensis* var. *rectimarginata* (7.1-4 K), *C. patagonica* (7.1-4 K), *C. tripinnata* (7.1-4 K), *Clavatisporites mutisii* (7.1-85 Pa–E), *Clavatriletes* (7.2-50 M), *C. disparilis* (7.1-100 K), *Clavifera* (7.1-5 K, 59 E, 64 E–O), *C. triplex* (7.1-17 K, 29 Pa), *Cnemidaria–Hemitelia* (4.1-23 M, 26 Pl; 5.1-10 O; 6.1-10 M, 13 Pl; 7.2-27 Pl; 7.6-23 Q), *Conbaculatisporites* (7.1-17 K), *Concavisporites* (7.1-42 E, 90 K), *C. jurienensis* (7.1-74 K), *C. lamontis* (5.1-3 K), *C.* cf. *laticrassus* (7.1-5 K), *C. stavensis* (5.1-5 E), *Concavissimisporites* (7.1-3 K), *C. minor* (7.1-74 K), *C. punctatus* (5.1-2 K; 7.1-74 K), *Contiginisporites cooksonii* (7.1-2, 3, 5, 10 K), *C. fornicatus* (7.1-3, 90 K), *Converrucosisporites* (7.1-2, 17 K), *C. proxigranulatus* (7.1-93 K), *C. saskatchewanensis* (7.1-74 K), *Coptospora* (7.1-2, 90 K), *C. foveolata* (7.1-5 K), *Corrugatisporites argentinus* (7.1-42, 46 E), *Couperisporites complexus* (7.1-3 K), *Crassoretitriletes vanraadshooveni* (7.2-39 Pl, 43, 50 M; 7.6-20 Q), *Crybelosporites* (7.1-10 K), *C.* cf. *brenneri* (7.1-99 K), *Ctenitis* (6.1-10 M; 7.2-16 M; 7.6-20 Q), *C. pleiosorus* (7.6-18 Q), *C. sloanei* (7.6-18 Q), *C. subincisa* type (7.6-20 Q), *Cyathea* (4.1-23 M, 26 Pl; 5.1-10 O; 6.1-7–10 M/M–Pl; 7.2-27 Pl; 7.6-13, 18, 20, 21, 23, 30, 32 Q), *C. colombiensis* (7.2-36 Pl), *C.* (*Nephelea*) *cuspidata* type (7.6-20 Q), *C. cyathifolia* (7.1-4 K), *C. escuquensis* type (7.6-20 Q), *C. frigida* type (7.6-20 Q), *C. horrida* type (7.6-20 Q), *C.* cf. *schanschin* (7.6-32 Q), *C.* (*Sphaeropteris*; 7.6-20 Q), *C.* (*Trichipteris*; 7.6-20 Q), Cyatheaceae (4.1-18 O; 6.1-16 Q, 19 Q; 7.6-17, 20 Q), *Cyatheacidites* (7.2-50 M; see Dettmann, 1986), *C. annulatus* (7.1-29 Pa, 42, 46 E, 49, 51, 52 O, 60 E; 7.2-8, 43 M), *C. tectifera* (7.1-3, 5 K), *C. vanderhammeni* (7.1-80, 81 K), *Cyathidites* (7.1-65 K/Pa; 7.2-45 M), *C. australis* (5.1-3 K; 7.1-2, 5, 55 K, 56 Pa, 59, 61 E, 90, 93, 99 K), *C. minor* (5.1-3 K; 7.1-5 K, 29 Pa, 42, 46 E, 49, 52 O, 55 K, 56 Pa, 59, 61 E, 64 E–O, 74, 90, 93, 99 K), *C. paleospora* (7.1-51, 52 O), *C. patagonicus* (7.1-29 Pa, 42 E, 52 O, 61 E), *C./Deltoidospora* (7.1-78d K), *Cyathoides thyrsopterioides* (7.1-58 E), *Cyclogranisporites* (7.1-74 K), *Cystopteris diaphana* type (7.6-20 Q), *C.–Hypolepis* (7.6-20 Q), *Danaea* (6.1-7 M, 18 Q; 7.2-27, 39 Pl), *Deltoidospora* (5.1-7a E; 7.1-2 K, 37 Pa, 42 E, 51, 52 O, 66 E–O, 80 K; 7.2-10 M), *D. adriennis* (7.2-43, 50 M), *D. australis* (7.1-19, 20 K), *D. hallii* (7.1-74, 99 K), *D. juncta* (7.1-74 K), *D. minor* (4.1-11 E, O/O–M; 5.1-2 K; 7.1-5, 17, 19, 20 K), *D. nana* (7.1-93 K), *D. neddeni* (7.1-19 K), *D. quiriquinaensis* (7.1-55 K), *D. tenuis* (7.1-99 K), *Dennstaedtia* (7.6-20 Q), *D. patagonica* (7.1-8, 14 K), *Densoisporites* (7.1-52 O, 99 K), *D. corrugatus* (7.1-3, 5 K), *D. microrugulatus* (7.1-93 K), *D. velatus*

(7.1-2, 3, 5 K), *Dicksonia* (7.6-23, 33 Q), *D. patagonica* (7.1-41 E), *D. sellowiana* type (7.6-20, 32 Q), *Dicksoniopsis coniopteroides* (6.1-1 K), *Dicranopteris* (4.1-26 Pl), *Dictyophyllidites* (5.1-2 K; 7.1-2 K, 33 Pa), *D. chiquimilense* (7.2-12 M), *D. concavus* (7.1-29 Pa), *D. equiexinus* (7.1-90 K), *D. harrisii* (7.1-74 K), *D. mortoni* (7.1-17, 19 K), *Discisporites discoides* (5.1-3 K), *Distaltriangulisporites* cf. *perplexus* (7.1-74 K), *Divisisporites* (7.1-50 O), *D.* cf. *maximus* (7.1-74 K), *Dorfiella auriculata* (4.1-2 K), *Dryopteris* (4.1-39/40 Q; 6.1-11 Q; 7.6-17 Q), *Dryopterites problematicus* (7.1-8, 14 K), *Duplexisporites* (7.1-2, 3 K), *Duplosporis* (7.1-55 K), *Echinatisporis* cf. *aculeatus* (4.1-10 E), *E. varispinosus* (7.1-74 K), *Echinatisporites* (4.1-11 E, O/O–M, 22 M), *E. bockwitzensis* (4.1-22 M), *E. brevispinosus* (7.1-85 Pa), *Echinosporis* (7.2-43, 50 M), *Echitriletes muelleri* (7.1-66 E/O, 100 K; 7.2-43, 50 M), *Elaphoglossum–Asplenium–Hemidictyum* (7.6-17, 20 Q), *Elaphoglossum carrioni* (7.2-30 M), *E. cuspidatum* (7.6-20 Q), *Elaterocolpites castelaini* (7.1-74, 78d K), *Elateroplicites africaensis* (7.1-78d K), *Elaterosporites klaszi* (7.1-74, 78d K), *E. verrucatus* (7.1-74 K), *Equisetites* (7.1-4, 97a K; 7.2-5 M), *Equisetum* (6.1-15 Pl/Pl–Q; 7.1-62 O; 7.2-16 M), *Eriosorus flexuosus* (7.6-20 Q), *Erlansonisporites sparis* (7.1-4 K), *Espora apiculata* (7.1-33 Pa), *Faveasporis areapunctatis* (7.1-52 O), *F. palaequetrus* (7.1-52 O), *Favososporites* (*Horstisporites*) *feruglioi* (7.1-7 K), *F. spinulosus* (7.1-7 K), fern spores (4.1-22 Pl, 29 Q), *Filicites* (7.1-15 E), *F. lojanus* (7.2-30 M), *Foraminisporis asymetricus* (7.1-5 K), *F. dailyi* (7.1-3, 5, 10 K), *F. microgranulatus* (7.1-3 K), *F. variornatus* (7.1-3 K), *F. wonthaggiensis* (7.1-3, 10, 74 K), *Foveotriletes* (7.1-90 K), *F.* cf. *labrus* (7.2-13 M), *F. margaritae* (7.1-85 Pa–E, 94 K; 7.2-43 M), *F. ornatus* (7.2-43, 50 M), *F. palaequetrus* (7.1-46 E, 49, 52 O), *Gabonisporis vigourouxii* (7.1-34, 35 Pa, 65 K–Pa, 100 K), *Gemmatriletes clavatus* (7.1-65 K–Pa, 74, 99 K), *G.* cf. *densegemmatus* (7.1-74 K), *Gleichenia* (7.1-9 K), *G. pectinataforma* (5.1-17 M), *Gleicheniidites* (5.1-3 K; 7.1-11, 20 K, 49 O, 59 E, 64 E–O), *G. apilobatus* (5.1-3 K; 7.1-90 K), *G. argentinus* (7.1-56 Pa), *G.* aff. *cercinidites* (7.1-2 K), *G. circinidites* (5.1-3 K; 7.1-52 O, 56 Pa), *G. marciae* (5.1-3 K), *G. senonicus* (5.1-2, 3 K; 7.1-5, 10, 17-19 K, 29 Pa, 42 E, 66 E–O), *G. severus* (5.1-3 K), *Gleichenites* (5.1-1 K), *G. argentinica* (7.1-4 K), *G. feruglioi* (7.1-4 K), *G. piatnitzkyi* (7.1-8, 14 K), *G. san-martinii* (7.1-4 K), *G. vegagrandis* (7.1-4 K), *Goniopteris* (7.2-25 Pl), *G. cochabambensis* (7.2-30, 34 M), *G. lojana* (7.2-30 M), *G. patagoniana* (7.1-41 E), *Grammitis* (6.1-10 M, 16 Q; 7.2-27 Pl; 7.6-17, 20, 23 Q), *G.* (*Ctenopteris*) *moniliformis* type (7.6-20 Q), *G. succinea* (5.1-14 M), *Granulatisporites* (7.1-17 K), *Grapnelispora* (7.1-20 K), *G. evansii* (7.1-18 K, 37 Pa), *Gymnogramma* (7.2-23, 25 Pl; 7.6-32 Q), *Gymnogramma* (*Hemionitis*) *wadii* (4.1-24 M), *G. woodringi* (5.1-16 M), *Gymnogramma* (?) (7.2-21 M), *Hamulatisporis* (7.1-17, 74 K), *H. hamulatis* (7.1-90 K), *Hausmannia papilio* (7.1-4 K), *H. patagonica* (7.1-4 K), *Heliosporites baculatus* (7.1-5 K; *Antulsporites baculatus*), *Hemitelia* (4.1-23 M; 6.1-18 Q), *H. brannerii* (5.1-8 O; 7.2-46 Pl), *Henrisporites elegans* (7.1-6 K), *H. heteracanthus* (7.1-7 K), *H. musacchioi* (cf. *Isoetes*; 7.1-6 K), *Histiopteris incisa* (7.6-20 Q), *Horriditriletes* (7.1-2 K), *Horstisporites feruglioi* (7.1-4 K), *H. iridodea* (7.1-4 K), *Hughesisporites patagonicus* (7.1-4 K), *H. rugulatus* (7.1-4 K), *Huperzia* (7.6-17 Q), *H.* (*Lycopodium*) *fuegiana* (7.6-12 Q), *H. selago* (7.6-9 Q), Hymenophyllaceae (7.6-12 Q), *Hymenophyllum* (4.1-38 Q; 6.1-13 Pl, 16 Q; 7.1-9 K; 7.2-27 Pl; 7.6-32 Q), *H. myriocarpum* (7.6-20 Q), *H. priscum* (7.1-8, 53 K), *H. trichophyllum* (7.6-20 Q), *Hypocrititriletes insolitus* (7.1-9 K), *Hypolepis hostilis* type (7.6-20 Q), *Impardecispora* (7.1-78d K), *I. trioreticulosa* (7.1-74 K), *Interulobites distannulatus* (7.1-3 K), *I. intraverrucatus* (7.1-3, 10 K), *I. pseudoreticulatus* (7.1-3 K), *I. triangularis* (7.1-2, 10 K), *I. variabilis* (7.1-19 K), *Intrapunctatisporites* (7.2-45 M), *Intrapunctosporis semipunctus* (7.1-87 E), *Ischyosporites* (7.1-17 K, 37 Pa), *I. areapunctatis* (7.1-49, 51, 52 O; 7.2-8 M), *I. problematicus* (7.1-85 Pa–E), Isoetaceae (4.1-18 O/O–M), *Isoetes* (4.1-32, 36 Q; 6.1-15 Pl/Pl–Q, 15 Q, 16 Q; 7.2-27 Pl; 7.6-12, 13, 15, 17, 21–23, 32, 33 Q), *I. boyacensis* (7.6-20 Q), *Isoetes* (?) *incerta* (5.1-8 O), *I. salvatieri* (7.6-12 Q), *Isoetites* (7.1-97a K), *Jamesonia* (6.1-16 Q; 7.6-15, 17, 20 Q), *Jamesonia–Eriosorus* (5.1-10 O), *Kirchheimerisporites tenuiradiatus* (7.1-85 Pa–E), *Klukisporites* (7.1-74 K), *K. elongatus* (7.1-93 K), *K. labiatus* (7.1-2 K), *K. pachydictyus* (7.1-17 K), *K. scaberis* (7.1-3, 99 K), *K. tuberosus* (7.1-3 K), *K. variegatus* (7.1-90, 100 K), *Kraeuselisporis* (7.1-74 K), *Kuylisporites waterbolkei* (7.2-43, 50 M), *Laevigatosporites* (4.1-11, 18 O/O–M; 5.1-3 K, 7 E, 20 M–P; 7.1-34, 35 Pa, 59 E, 64 E–O, 74 K), *L. belfordii* (7.1-3, 5 K), *L. catanejensis* (7.2-43, 50 M), *L. dehiscens* (7.1-55 K), *L. discordatus* (7.1-17 K, 87 E), *L. gracilis* (7.1-17, 93 K), *L. haardtii* (5.1-5 E), *L. nutidus* (7.1-87 E), *L. ovatus* (5.1-3 K; 7.1-5, 16, 17, 20 K, 29 Pa, 42, 46 E, 49, 51, 52 O, 56 Pa; 7.2-13 M), *L. tibuensis* (7.1-85 Pa–E), *L. vulgaris* (7.1-17 K, 61 E; 7.2-43 M), *Leiotriletes* (7.1-16, 55 K, 59 E, 64 E–O; 7.2-10 M), *L. giganteus* (7.1-80 K), *L. guaduensis* (7.1-81, 82 K), *L. regularis* (7.1-5 K, 29 Pa, 42 E, 52 O), *Lepidosorus* (4.1-22 M), *Leptolepidites* (7.1-17, 78d K), *L. densus* (7.1-42 E), *L. macroverrucosus* (7.1-3 K), *L. major* (7.1-5, 90 K), *L. proxigranulatus* (7.1-3, 10 K), *L. psarosus* (7.1-99 K), *L. verrucatus* (7.1-90 K), *Lindsaea* (7.6-23 Q), *Lomariopsis* (4.1-26 Pl), *L. tertiaria* (7.2-21 M, 23, 25 Pl), *Lophosoria* (6.1-13 Pl, 16 Q; 7.2-16 M; 7.6-23 Q), *L. quadripinnata* (7.6-12, 20, 32 Q), *Lycopodium* (4.1-18 O/O–M, 23 M, 26 Pl; 5.1-10 O; 6.1-7, 9–11 M/M–Pl, 13 Pl, 15 Q, 16 Q, 18 Q; 7.2-27 Pl; 7.6-7, 13, 17, 20, 21, 23 Q), *L. alopecuroides* (7.6-32 Q), *L. cernuum* (7.6-18, 20, 31 Q), *L.* cf. *clavatum* (7.6-18, 32 Q), *L. cuatrecasasii* (7.6-20 Q), *L. curvatum* type (7.6-20 Q), *L. foveolate* (7.6-20–23, 32 Q), *L. jussiaei* type (7.6-20 Q), *L. magellanicum* (7.6-2 Q), *L. passerinoides* (7.6-18 Q), *L. trianae* (7.6-31 Q), *Lycopodiumsporites* (7.1-17, 78d, 80 K), *L. austroclavatidites* (7.1-2 K, 29 Pa, 42, 46 E, 51, 52 O–M), *L. clavatoides* (5.1-3 K), *L. eminulus* (7.1-42, 47 E), *L. facetus* (7.1-99 K), *L. novomexicanum* (7.1-66 E–O, 100 K), *L. paleocenicus* (7.1-90 K), *Lygodioisporites* (7.1-80 K), *Lygodium* (5.1-23 Q; 6.1-7 M), *L. bifidium* (7.2-30 M), *Lygodiumsporites* (7.1-2 K), *L. adriennis* (4.1-9 E; 5.1-5, 7 E), *Magnastriatites grandiosus* (7.2-43, 50 M), *M. howardii* (7.1-100 K, *Ceratopteris*), *Marattia* cf. *verschaffeltiana* (7.6-32 Q), *Marattisporites scabratus* (7.1-17 K), *Matonisporites* (7.1-10 K, 29 Pa, 99, 100 K; 7.2-45 M), *M.* cf. *dorogensis* (7.1-93 K), *M. equiexinus* (7.1-93 K), *M. guianensis* (7.1-93 K), *M. mulleri* (7.2-50 M), *M. ornamentalis* (7.1-49, 51, 52 O), *M. tenuilabratus* (7.1-2, 3 K), *Meniscium* [*Thelypteris*] *wolfi* (7.2-32 M), *Mesosingeria mucronata* (7.1-4 K), *M.* (?) *obtusa* (7.1-4 K), *M. striata* (7.1-4 K), *Microfoveolatosporis* (5.1-2 K; 7.1-5, 74 K), *M. skottsbergii* (7.1-85 Pa–E), *Minerisporites* (7.1-74 K), *M. cheblii* (7.1-6 K; *Isoetes*), *M. elegans* (7.1-4 K), *M.*

holobrochatus (7.1-7 K), *M. laceratus* (7.1-4 K), *M. patagonicus* (7.1-4 K), monolete fern spores (4.1-21 O/O–M, 26 Pl; 5.1-10 O, 20 M; 6.1-2 E; 7.1-10 M), *Monolites alveolatus* (7.1-49 O), *Monosulcites* (7.1-90 K), *Muerrigerisporis americanus* (7.1-80 K), *M.*(?) *sanadriensis* (5.1-2 K), *Muricingulisporis* (7.1-2 K), *M. annulatus* (7.1-3, 5 K), *M. chenquensis* (7.1-46 E, 51, 52 O; 7.2-8 M), *M. verrucosus* (7.2-12 M), *Naiaditaspora gemmata* (7.1-5 K), *Neoraistrickia* (7.1-5, 17 K, 29 Pa, 74 K), *Nephrolepis* (7.6-18 Q), *Nijssenosporites fossulatus* (7.2-43 M), *Nodosisporites* (7.1-10 K), *Obtusisporis obtusangulus* (7.1-5 K), cf. *Onychium* (7.6-20 Q), *Ophioglossum* (6.1-10 M, 16 Q), *O. crotalophoroides* (7.6-20 Q), *O. engelmannii* type (7.6-20 Q), *Ornamentifera tuberculata* (7.1-5 K), *Ornatisporites* aff. *dentatus* (5.1-5 E), *Osmunda* (6.1-11 Q; 7.6-32 Q), *Osmundacidites* (7.1-66 E–O; 7.2-45 M), *O. diazii* (7.1-5 K), *O. minor* (7.1-85 Pa–E), *O. wellmanii* (7.1-2, 74 K), *Paesia viscosa* (7.6-20 Q), *Paleoazolla patagonica* (7.1-21 Pa), *Pecopteris* (7.1-15 E; 7.2-21 M, 23 Pl), *P. buhsei* (7.1-58 E), *Perinomonoletes* (7.2-43, 50 M), *Peromonolites* (7.1-42, 59 E, 64 O), *P.* cf. *boweni* (7.1-56 Pa), *P. fragilis* (7.1-93 K), *P. radiatus* (7.1-49 O), *P. vellosus* (7.1-46 E, 49, 51, 52 O), *Perotriletes* (7.1-66 E/O), *P. pannuceus* (7.1-78d, 90, 99, 100 K), *Phlebopteris* (7.1-74 K), *Pilosisporites trichopapillosus* (7.1-93 K), *Pilularia* (7.6-20 Q), *Pityrogramma* (4.1-26 Pl; 6.1-13 Pl; 7.6-18, 20, 21, 23 Q), *P.–Pteris altissima* type (7.6-20 Q), *Planisporites* (7.1-85 Pa–E), *Pleopeltis* (*Microgramma*) *ciliata* (7.6-20 Q), *Polycingulatisporites trabeculatus* (7.1-3 K), Polypodiaceae (–Blechnaceae–Pteridaceae) (4.1-18 O/O–M; 6.1-15 Pl/Pl–Q, 19 Q; 7.6-7, 18 Q), *Polypodiaceaesporites* (7.2-45 M), *Polypodiaceoisporites* (7.2-50 M), *P. elegans* (7.1-5 K), *P.* (?) *fossulatus* (7.1-85 Pa–E), *P. potoniei* (7.1-66 E/O, 100 K), *P. pseudopsilatus* (7.2-43 M), *P.* cf. *speciosus* (7.2-43 M), Polypodiales (7.2-39 Pl), *Polypodiidites–Polypodiisporites–Polypodiisporonites* (4.1-22 Pl; 7.1-2, 5, 17 K, 46, 91 E), *P. alienus* (4.1-11 O/O–M; 5.1-5 E), *P. echinatus* (7.1-85 Pa–E), *P. flavus* (4.1-11 E, 22 M; 5.1-5 O/O–M), *P. inangahuensis* (7.1-50–52 O, 55 K, 85 Pa–E), *P. megaflavus* (4.1-11 O/O–M), *P. minimus* (7.1-52 O), *P. pachyexinatus* (7.1-85 Pa–E), *P. radiatus* (7.1-51, 52 O), *P. speciosus* (7.1-42 E, 85 Pa–E), *P.* cf. *tenellis* (4.1-11 O/O–M), *P. undulatus* (4.1-22 M), *Polypodium* type (4.1-23 M, 32 Q; 5.1-23 Q; 6.1-15 Pl/Pl–Q; 7.1-61 E; 7.6-20, 22, 23 Q), *P. adnatum* (7.6-20 Q), *P. aureum* (7.6-18, 20 Q), *P. feuillei* (7.6-12 Q), *Polystichum bolivianum* (7.2-23–25 Pl), *Psilamonoletes tibui* (7.2-50 M), *Psilatriletes circumundulatus* (7.1-93 K), *P. lobatus* (7.2-50 M), *P. peruanus* (7.2-50 M), *P.* sp. 1, 2 (7.2-50 M), *Psilotum* (4.1-26 Pl), *Pteridacidites* (7.1-85 Pa–E), *Pteridium* (4.1-36 Q; 6.1-11Q; 7.6-17 Q), *Pteris* (4.1-21 O/O–M, 23 M; 5.1-10 O, 20 M, 23 Q; 6.1-2 E, 7–10 M, 13, 14 Pl; 7.2-27 Pl; 7.6-21, 23, 31, 32 Q), *P. cousiniona* (7.1-58 E; 7.2-19a M), *P. dentata* (4.1-9 E; 5.1-7 E), *P. frenguellii* (7.1-15 E), *P. grandifolia* type (7.6-20 Q), *Punctatiosporites* (7.1-55 K), *P. major* (7.1-74 K), *Punctatisporites scabratus* (7.1-74 K), *Pustulatisporites* (7.1-20 K), *Quiriquinaspora chilensis* (7.1-55 K), *Regulatisporites mallatus* (7.1-52 O), *Reticulatisporites* (7.1-2, 80 K), *R. ornatus* (7.1-5 K), *Reticuloidosporites tenellis* (7.1-42 E, 51, 52 O), *Retimonocolpites* (7.1-90 K), *Retitriletes* (7.1-74 K, 85 Pa–E), *R. austroclavaidites* (7.1-5, 19 K, 34, 35 Pa, 49 O), *R. baqueroense* (7.1-5 K), *R. sommeri* (7.2-43 M), cf. *Rhipidopteris–Elaphoglossum* (6.1-15 Pl/Pl–Q), *Rotverrucosisporites* (7.1-2, 3 K), *R. labratus* (7.1-5 K), *Rotverrusporites rupunniensis* (7.1-93 K), *Rouseisporites* (7.1-11 K, 49 O), *R. reticulatus* (7.1-5 K), *Ruffordia goepperti* (7.1-4 K), *Rugotriletes* (7.2-50 M), *Rugulatisporites neuquenensis* (7.1-5 K), *Saccoloma domingene* type (7.6-20 Q), *S. elegans* type (7.6-20 Q), *Salvinia* (6.1-15 Pl/Pl–Q), *S. coahuiensis* (4.1-3 K), *S. lechmanni* (7.2-32 M), *Scabramonoletes* (?) (7.1-85 Pa–E), cf. *Schizaea* (7.6-20 Q), *Schizea certa* (7.1-90, 100 K), *S. reticulata* (7.1-90 K), Schizaeaceae (7.1-97a K), *Schizaeoisporites* (7.1-3 K), *S. cicatricos* (7.1-80 K), *S. rectangularis* (7.1-80 K), *Schizosporis* (7.1-80 K), *S. paleocenicus* (7.1-56 Pa), *S. rugulatus* (7.1-56 Pa), *Selaginella* (4.1-9 E, 21 O/O–M, 23 M, 26 Pl, 32, 34 Q; 5.1-10 O, 23 Q; 6.1-2 E, 18 Q, 23 Q; 7.2-39 Pl; 7.6-20, 23 Q), *S. anceps* type (7.6-20 Q), *S.* cf. *excurens* (7.6-32 Q), *S. sellowii* (7.6-20 Q), Selaginellaceae (4.1-18 O/O–M), *Sergipea* (7.1-74 K), *S. naviformis* (7.1-90, 99 K), *S. variverrucata* (7.1-99 K), *Sestrosporites* (7.1-2 K), *S. pseudoalveolatus* (7.1-5, 74 K), *Sphaen[r]opteris molinae* (7.1-15 E), *Sphaeropteris–Trichipteris* (4.1-21 O/O–M, 26 Pl; 6.1-2 E), *Sphenopteris* cf. *fittonii* (7.1-4 K), *S. goepperti* (7.1-4 K), *S. patagonica* (7.1-4 K), *S.* (*Onychiopsis*) *psilotoides* (7.1-4 K), *Staplinisporites caminus* (7.1-2, 3, 5 K), *Stereisporites antiquasporites* (7.1-17 K), *S. crassiancoris* (4.1-10 E), *S. microgranulus/crassiexinus* (4.1-10 E), *S. pilatus* (7.1-99 K), *S. stereoides* (5.1-2 K), *Stoverisporites lunaris* (7.1-5 K), *Taurocusporites reduncus* (5.1-3 K), *T. segmentatus* (7.1-3, 5, 10 K), *Thecaspora spinosa* (7.1-67, 68 K), *Thelypteris* (7.6-20 Q), *T. pilosula* (7.6-18 Q), *Thyrsopteris antiqua* (7.1-8, 53 K), *Todiosporites* (7.1-52 O), *T. major* (7.1-17, 19 K, 50 O, 99 K), *T. minor* (5.1-3 K; 7.1-19 K), *Trichomanes* (6.1-20a Q), *Triletes*, trilete fern spores (4.1-22 Q, 26 Pl; 5.1-7 E, 10 O, 20 M, 23 Q; 6.1-2 E, 7, 10 M; 7.1-60 E, 63 O, 99, 100 K), *T. fasolae* (7.1-42 E), *T. parvallatus* (7.1-29 Pa, 42, 46 E, 52 O, 55 K), *T. tuberculiformis* (7.1-2 K, 60 E; 7.2-13 M), *Trilobosporites* (7.1-2 K), *T. apiverrucatus* (7.1-3, 5 K), *T. canadensis* (7.1-3 K), *T. purverulentus* (7.1-3, 5 K), *T. trioreticulosus* (7.1-5, 10 K), *Triporoletes reticulatus* (7.1-3, 10 K), *Tuberculatosporites* (7.1-5, 99 K), *T. parvus* (7.1-29 Pa, 42 E), *Tuberositriletes verrucatus* (7.1-85 Pa–E), *Undulatisporites concavus* (5.1-7 E), *U. takutuensis* (7.1-93 K), *U. undulapolis* (4.1-22 M; 7.1-93 K), *Uvaesporites* (7.1-74, 78d K), *Vallizonosporites spinosus* (7.1-5 K), *Velosporites* (7.1-90 K), *Verrucatosporites* (7.2-45 M), *V. favus* (4.1-10 E), *V. megafavus* (4.1-10 E), *V.* cf. *speciosus* (7.2-43 M), *V. usmensis* (5.1-7 E; 7.1-66 E–O, 87 E; 7.2-43, 50 M), *Verrucatotriletes* cf. *bullatus* (7.2-43, 50 M), *Verrucosisporites* (7.1-3, 5, 10 K, 61 E, 90 K), *V. kopukeunsis* (7.1-52 O), *V. rotundus* (7.1-74 K), *Verrutriletes* (7.2-50 M), *V. tomtaylori* (7.1-4 K), *Vitreisporites pallidus* (7.1-93 K), Vittariaceae (cf. *Antrophyum*; 4.1-21 O/O–M), *Waltzispora* (7.1-17 K), *Weichselia reticulata* (7.1-74 K), *Woodwardia* (7.1-15 E), *Zlivisporis* (7.1-67, 68 K), *Z. blanensis* (7.1-85 Pa–E, 100 K), *Zonalapollenites* [?, spore] (7.1-90 K). Incertae sedis: *Filicites* (7.2-16 M).

Gymnosperms

Araucariaceae (7.2-8 M): *Araucaria* (4.1-1 K; 7.1-15 E; 7.2-16, 17 M), *A. angustifolia* (7.6-33 Q), *A. araucoensis* (7.1-58 E), *A. grandifolia* (7.1-4 K), *A. nathorstii* (7.1-15 O), *A. pichileufensis* (7.1-41 E), *Araucariostrobus* (7.1-97a K).

Coniferales (7.1-97a K).

Cupressaceae (4.1-30 Q; 6.1-11 Q; 7.6-7, 32 Q): *Austrocedrus* (7.2-17 M), *Cupressus–Juniperus–Taxodium* (4.1-18 O/O–M, 32–34, 36, 37, 39/40 Q), *Fitzroya tertiaria* (7.1-41 E; 7.2-5 M), *Juniperus* (4.1-29 Q; 5.1-21 Q; 6.1-1 Q), *J. californica* (4.1-28 Q), *Lepidothamnus* (*Dacrydium*) *fonckii* (7.6-2, 9 Q), *Libocedrus prechilensis* (7.1-41 E), *Pilgerodendron* (*Libocedrus*) type (7.6-9, 12 Q).

Cycadaceae: Cycadaceae (4.1-23 M), Cycadales (7.1-97a K), *Zamia* (7.2-30 M), *Z. collazoensis* (5.1-8 O), *Z. noblei* (5.1-8 O), *Z. tertiaria* (7.1-41, 58 E; 7.2-19a M).

Ephedraceae: *Ephedra* (4.1-18 O/O–M, 30 Q; 6.1-11 Q; 7.1-58 E; 7.2-19a M; 7.6-4–8, 11–13, 17 Q), *E. frustillata* (7.6-2 Q), *E. nevadensis* (4.1-28, 29 Q), *E. trifuca* type (4.1-29 Q).

Ginkgoaceae: *Ginkgo* (?) (7.1-15 O), *G. patagonica* (7.1-41 E).

Gnetales (7.1-97a K).

Pinaceae: *Abies* (4.1-18 O/O–M, 26 Pl, 29, 30–34, 36, 38 Q; 6.1-15 Pl/Pl–Q), *Picea* (4.1-18, 21 O/O–M, 26 Pl, 30–33 Q; 6.1-11 M–Pl), *Pinus* (4.1-18, 20 O/O–M, 22, 23 M, 26 Pl, 29, 40 Q; 5.1-20 M, 24 Q; 6.1-1–3 Q, 5–8 Q, 11 M/M–Pl, 12 Pl, 11–14 Q, 15 Pl/Q, 17 Q; 7.6-32, 33 Q), *P. caribaea* (5.1-21–23 Q), *P. edulis/remota* (4.1-28 Q), *P. tropicalis* (5.1-23 Q; aff. *tropicalis* 5.1-9 O), *Tsuga* (4.1-32 Q).

Podocarpaceae (7.2-8 M; 7.6-15, 17, 18 Q): *Acmopyle antarctica* (7.1-53 K), *Dacrydium* (4.1-18 O/O–M; 7.1-9 K; 7.2-17 M), *Decussocarpus* [*Podocarpus*?] (7.2-39 Pl), *Lepidothamnus* (*Dacrydium*) *fonckii* (7.6-2, 9 Q), cf. Podocarpaceae (7.1-5 K), *Podocarpus* (4.1-18, 20 O/O–M, 26 Pl, 32 Q; 5.1-10 O; 6.1-2 Q, 3 Q, 5 Q, 6 Q, 10 M, 11 Q, 13 Pl, 13–18 Q; 7.1-9 K, 94 O–M; 7.2-16, 17 M, 39 Pl; 7.6-7, 8, 21–25, 28, 29, 31–33 Q), *P. andiniformis* (7.1-41 E), *P. angustifolius* (5.1-23 Q), *P. boliviensis* (7.2-25 Pl), *P. dubius* (7.1-4 K), *P. engelhardti* (7.1-41 E), *P. fossilis* (7.2-21 M, 23–25 Pl), *P. inopinatus* (7.1-8, 53 K, 57 E), *P. nubigena* (7.6-2, 9, 12 Q), *P.? palissyafolia* (7.1-4 K), *P. tertiaria* (7.1-8 K), *Podocarpus–Prumnopitys* (7.2-27 Pl), *Saxegothaea* (7.6-7 Q), *S. conspicua* (7.6-9, 12 Q).

Taxaceae: *Acmopyle antarctica* (7.1-8, 53 K), *A. engelhardti* (7.1-15 E).

Taxodiaceae: *Sequoia chilensis* [?] (7.1-58 E; 7.2-19a M), *Taxodium* (4.1-31 Q).

Welwitschiaceae: *Cratonia cotyledon* (7.1-97a K), *Welwitschiella austroamericana* (7.1-97a K), *Welwitschiophyllum brasiliense* (7.1-97a K), *Welwitschiostrobus murili* (7.1-97a K).

Other gymnosperms: *Aachenia knoblochi* (4.1-4 K), *Abietineaepollenites* (4.1-11 E, O/O, M; 7.1-93 K), ?*Alaticolpites limai* (7.1-99 K), *Alisporites* (7.1-2, 10 K), *A. australis* (7.1-20 K), *A. bilateralis* (5.1-3 K), *Alkastrobus peltatus* (7.1-2 K), *Allicospermum patagonicum* (7.1-4 K), *Almargemia incrassata* (7.1-4 K), *Applanopsis dampieri* (7.1-74 K), *A. segmentatus* (7.1-74 K), *A. trilobatus* (7.1-74 K), *A. turbatus* (7.1-74 K), *Apterocladus lanceolatus* (7.1-4, 5 K), *Araucariacites* (7.1-5, 12 K, 59 E, 81 K, 85 Pa–E), *A. australis* (5.1-2 K; 7.1-2, 20 K, 43, 46 E, 49, 51, 52 O, 56 Pa, 61 E, 65 K–Pa, 66 E–O, 74, 78d, 93, 100 K), *A. guianensis* (7.1-74, 93, 99 K), *A. limbatus* (5.1-3 K; 7.1-99 K), *Araucarioxylon chilense* (7.2-18 M), *A. doeringii* (7.1-54 K), *A. kellerense* (7.1-54 K), *A. ohzuanum* (7.1-54 K), *A. parachoshiense* (7.1-54 K), *A. pichasquense* (7.1-54 K), *A. pseudoparenchymatosum* (7.1-54 K), *A. quiriquineanum* (7.1-54 K), *Araucarites* (6.1-1 K), *A. baqueroensis* (7.1-4 K), *A. minimus* (7.1-4 K), *Assamiapollenites incognitus* (7.1-49 O), *Atrotaxis ungeri* (7.1-4 K), *Balmeiopsis* (7.1-5 K), *B. limbatus* (7.1-3, 74 K), *Bennettitaepollenites minimus* (7.1-99 K), Bennettitiales (7.1-97a K), *Bororoa andreisii* (7.1-24 Pa), *B. anzulovichii* (7.1-24 Pa), *Brachyphyllum* (4.1-1, 5 K; 5.1-1 K; 7.1-5, 74, 97a K), *B. brettii* (7.1-4 K), *B. irregulare* (7.1-4, 5 K), *B. mamillare* (7.1-1 K), *B. mirandai* (7.1-4 K), *B. mucronatum* (7.1-4 K), *B. tigrense* (7.1-4 K; with *Podocarpidites*-type pollen), *Brunoa santarosensis* (7.1-12 K), *Callialasporites* (7.1-5 K), *C. dampieri* (7.1-10, 78d K), *C. trilobatus* (7.1-2, 19, 20 K), *Cedridites* (7.1-66 E–O), *Cedripites* (4.1-11 E, O/O–M), *Cerebropollenites macroverrucosus* (7.1-74 K), *C. mesozoicus* (7.1-93 K), *Circulina minima* (7.1-99 K), *C. parva* (7.1-99 K), *Classopollis* (7.1-2, 10, 12, 20, 65, 74, 78d K), *C. classoides* (7.1-19 M, 100 K), *C. intrareticulatus* (7.1-99 K), *C. jardinei* (7.1-90 K), *C. obidosensis* (7.1-90 K), *C. torosus* (7.1-90, 93, 99 K), *Coptospora striata* (7.1-3 K), *Corollina* (7.1-10 K), *Ca(o)rollina torosus* (4.1-11 E, O/O–M), *Cupressinocladus leptocaldoides* (7.1-74 K), *C. pompeckji* (7.1-74 K), *Cupressioxylon mochaense* (7.1-54 K), *C. parenchymatosum* (7.1-54 K), *Cycadolepis baqueroensis* (7.1-4 K), *C. coriacea* (7.1-4 K), *C. involuta* (7.1-4 K), *C. lanceolata* (7.1-4 K), *C. menendezii* (7.1-4 K), *C. oblonga* (7.1-4 K), *C. petriellai* (7.1-4 K), *Cycadopites* (4.1-11 O/O–M; 5.1-2 K; 7.1-29 Pa), *C. adjectus* (7.1-56 Pa), *C.* cf. *fragilis* (7.1-93 K), *C. granulatus* (7.1-20 K), *C. minimus* (7.1-74 K), *C. nitidus* (7.1-2 K, 56 Pa, 74, 99 K), *Cyclusphaera* (?; 7.1-10), *C. crassa* (7.1-3 K), *C. patagonica* (7.1-3 K), *C. psilata* (7.1-3, 5 K), *C. radiata* (7.1-3 K), *Dacrycarpites australiensis* (7.1-12 K, 43 E, 52 O), *Dacrydiumites florinii* (7.1-12, 16 K, 43 E, 50 O, 56 Pa), *Dictyozamites areolatus* (7.1-4 K), *D. grandis* (7.1-4 K), *D. latifolius* (7.1-4 K), *D. minusculus* (7.1-4 K), *Elatocladus* (7.1-4 K), *Ephedripites* (7.1-19, 80, 81, 93 K), *E. ambonoides* (7.1-90 K), *E. barghoornii* (7.1-65 K–Pa, 78d, 90 K), *E. jansonii* (7.1-65 K–Pa), *E. montanaensis* (7.1-65 K–Pa), *E. multipartitus* (7.1-50 O), *E. notensis* (7.1-56 Pa), *E. pentacostatus* (7.1-100 K), *E. procerus* (7.1-90 K), *E. strigatus* (7.1-65 K–Pa, 90 K), *E. subtilis* (7.1-100 K), *E. undulatus* (7.1-100 K), *E. validus* (7.1-90 K), *E. vanegensis* (7.1-85 Pa–E, 96 Pa; gymnosperm, Araceae), *Equisetosporites* (4.1-11 O/O–M), *E. ambiguus* (7.1-74 K), *E. claricristatus* (7.1-49, 51, 52 O; 7.2-8, 10, 13 M), *E. concinnus* (7.1-99 K), *E. costaliferous* (7.1-74, 99 K), *E. dudarensis* (7.1-74 K), *E. elongatus* (7.1-99 K), *E. fragilis* (7.1-99 K), *E. fusiformis* (7.2-13 M), *E. irregularis* (7.1-99 K), *E. leptomatus* (7.1-74 K), *E. lusaticus* (7.1-52 O; 7.2-10, 13 M), *E. minuticostatus* (7.1-20, 99 K), *E. mollis* (7.1-74 K), *E. multicostatus* (7.1-20 K), *E. notensis* (7.1-43 E, 49, 52 O; 7.2-10, 13 M), *E.* cf. *procerus* (7.1-99 K), *E. strigatus* (7.1-99 K), *E.* cf. *subcircularis* (7.1-74, 99 K), *E. translucidus* (7.1-74 K), *Eucommiidites* (5.1-3 K; 7.1-90 K), *E. minor* (7.1-74, 78d, 93 K), *E. troedsonii* (5.1-2 K; 7.1-93 K), *Exesipollenites tumulus* (7.1-93, 99 K), *Frenelopsis* (5.1-1 K), *Gamerroites psilasaccus* (7.1-5, 19 K, 46 E, 49, 51, 52 O), *G. volkheimeri* (7.1-5 K), *Ginkgoites ticoensis* (7.1-4 K), *G. tigrensis*

(7.1-4 K), *Gliscopollis* (7.1-2 K), *Gnetaceapollenites* (7.1-90 K), *G. boltenhagenii* (7.1-74 K), *G. clathratus* (7.1-100 K), *G. crassipoli* (7.1-100 K), *G. diversus* (7.1-100 K), *G. jansonii* (7.1-99 K), *G. oreadis* (7.1-99 K), *G. retangularis* (7.1-99 K), *G. similis* (7.1-100 K), *Inaperturopollenites* (7.1-34, 35 Pa, 78d, 81, 99 K), *I. dubius* (5.1-3 K; 7.1-74 K), *I. giganteus* (7.1-93 K), *I. hiatus* (5.1-2, 3 K; 7.1-52 O), *I. laevigatus* (7.1-55 K), *I. microclavatus* (7.1-100 K), *I.* aff. *scabratus* (5.1-2 K), *I. simplex* (7.1-100 K), *Karkenia incurva* (7.1-4 K), *Kobalostrobus olmosensis* (4.1-6 K), *Ktalenia circularis* (7.1-4 K), *Lindleycladus* (7.1-97a K), *Lygistepollenites florinii* (7.1-46 E, 49, 51, 52 O), *Menucoa cazaui* (7.1-23 Pa), *Mesembrioxylon* (7.1-24 Pa; Podocarpaceae or angiosperm fide original author, p. 159), *Mesodescolea plicata* (7.1-4 K), *Mesosingeria coriacea* (7.1-4 K), *M. herbstii* (7.1-4 K), *M. mucronata* (7.1-4 K), *M.* (?) *obtusa* (7.1-4 K), *M. parva* (7.1-4 K), *M. striata* (7.1-4 K), *Metapodocarpoxylon libanoticum* (7.1-74 K), *Microcachryidites* (7.1-20 K), *M. antarcticus* (7.1-2, 11, 12, 19 K, 43 E, 49–52 O, 56 Pa), *Monocolpopollenites* (7.1-99 K), *Monosulcites* (7.1-78d K), *M. chaloneri* (5.1-3 K; 7.1-99 K), *M.* cf. *granulatus* (7.1-16 K), *M. inspissatus* (5.1-3 K), *M. minimus* (5.1-3 K; 7.1-56 Pa, 65 K–Pa), *M. pseudospinosus* (7.1-16 K), *Morenoa fertilis* (7.1-4 K), *Nilssonia clarki* (7.1-4 K), *Nothopehuen brevis* (7.1-4 K), nucellus of *Caytonia* (7.1-74 K), orbiculas (7.1-5 K), *Otozamites archangelskyi* (7.1-1 K), *O. ornatus* (7.1-4 K), *O. parviauriculata* (7.1-4 K), *O. waltonii* (7.1-4 K), *Pachypteris elegans* (7.1-4 K), *P.* (?) *patagonica* (7.1-4 K), *Parvisaccites majesticus* (5.1-3 K), *P. radiatus* (5.1-3 K; 7.1-55 K), *Peltandipites* (7.1-99 K), *Peneterapites mollis* (7.1-99 K), *Phoenicopsis* cf. *speciosa* (5.1-1 K), *Phrixipollenites* (7.1-20 K), *Phyllocaldoxylon antarcticum* (7.1-54 K), *P. aparenchymatosum* (7.1-54 K), *Phyllocladidites mawsonii* (7.1-12 K, 43, 46, 47 E, 49, 51, 52 O, 55 K, 60 E), *P. ruei* (7.1-43 E), *P.* cf. *verrucosus* (7.1-46 E, 51 O), *Piceapollenites* (7.1-55 K), *P. alatus* (5.1-3 K), *Pinuspollenites concepcionensis* (7.1-55 K), *Platysaccus elizabethae* (5.1-3 K), *Podocarpidites* (7.1-10, 12 K, 59 E, 63, 64, 66 E–O, 100 K; 7.2-43, 45, 50 M), *P. elegans* (7.1-43, 46 E, 49, 51, 52 O; 7.2-10 M), *P.* cf. *ellipticus* (7.1-2 K, 46 E, 49, 52 O; 7.2-10 M), *P.* cf. *exiguus* (7.1-46 E, 52 O), *P. magnus* (7.1-43 E), *P. marwickii* (7.1-12, 16, 19 K, 31–35 Pa, 43 E, 49–52 O, 61 E; 7.2-13 M), *P. microreticuloidata* (7.1-12 K, 43 E), *P. multesimus* (7.1-55 K), *P. otagoensis* (7.1-56 Pa, 61 E), *P. psilasaccus* (7.1-12 K), *P. rugulosus* (7.1-19 K, 43, 46 E, 49, 52 O; 7.2-13 M), *P. verrucosus* (7.1-19 K, 50 O), *P.* sp. (7.1-12 K), *Podocarpoxylon* (4.1-5 K), *P. paleoandium* (7.1-54 K), *P. paleosalignum* (7.1-54 K), *Podosporites microsaccatus* (7.1-11 K), *Podozamites* (7.1-74 K), *P.* cf. *eichwaldii* (5.1-1 K), *Pristinuspollenites* (4.1-11 E, O/O–M), *Protodiploxypinus* (7.1-50 O), *Protophyllocladoxylon rosablancaense* (7.1-73, 74 K), *Protophyllocladus australis* (7.1-8, 14 K), *Proxapertites* (7.1-80, 81 K), *Pseudoaraucaria valentini* (7.1-8, 53 K), *Pseudoctenis* (7.1-74 K), *P. crassa* (7.1-4 K), *P. dentata* (7.1-4 K), *P. ensiformis* (7.4-4 K), *P. giganteus* (7.1-4 K), *P. ornata* (7.1-4 K), *Pterophyllum trichomatosum* (7.1-4 K), *Pteruchipollenites crenulatus* (5.1-3 K), *P. transversus* (5.1-2 K), *Ptilophyllum acutifolium* (7.1-4 K), *P. angustus* (7.1-1 K), *P. hislopii* (7.1-4 K), *P. longipinnatum* (7.1-4 K), *Raritania* (4.1-6 K), *Ruflorinia papillosa* (7.1-4 K), *R. pilifera* (7.1-4 K), *R. sierra* (7.1-4 K), *Saxegothopsis* (7.2-16, 17 M), *Singhia minima* (7.1-99 K), *S. montanaensis* (7.1-99 K), *Spheripollenites psilatus* (5.1-3 K; 7.1-56 Pa, 65 K–Pa), *S. subgranulatus* (7.1-74 K), *Squamastrobus tigrensis* (7.1-4 K), *Steevesipollenites alatiformis* (7.1-100 K), *S. amphoriformis* (7.1-100 K), *S. binodosus* (7.1-100 K), *S. cupliformis* (7.1-99 K), *S. duplibaculatus* (7.1-100 K), *S. giganteus* (7.1-100 K), *S. grambasti* (7.1-99 K), *S. multilineatus* (7.1-100 K), *S. nativensis* (7.1-100 K), *Sueria elegans* (7.1-4 K), *S. rectinervis* (7.1-4 K), *Taeniopteris* (7.1-4 K), *Tarphyderma glabra* (7.1-4 K), *Taxodiaceapollenites* cf. *hiatus* (7.1-65 K–Pa), *Taxodioxylon* (4.1-5 K), *T. pseudocompressum* (7.1-54 K), *Ticoa harrisii* (7.1-4 K), *T. lamellata* (7.1-4 K), *T. marginipinnulata* (7.1-4 K), *Tomaxellia biforme* (7.1-4 K, with *Classopollis* pollen; 7.1-5 K), *T. degiustoi* (7.1-4 K), *Triangulopsis* (7.1-99 K), *Trifossapollenites* (7.1-74 K), *Trisaccites* (7.1-59 E), *T. microsaccatus(m)* (7.1-10, 12, 16 K, 43, 46 E, 49, 51, 52 O, 55 K, 56 Pa, 61 E), *Trisacocladus tigrensis* (7.1-4, 5 K), *Tsugaepollenites mesozoicus* (7.1-55 K), *Vitreisporites pallidus* (5.1-3 K; 7.1-2 K), *Williamsonia bulbiformis* (7.1-4 K), *W. umbonata* (7.1-4 K), *Worsdellia bonettiae* (7.1-12 K), *Yuccites* (5.1-1 K), *Zamites* cf. *buchianus* (5.1-1 K), *Z. decurrens* (7.1-4 K), *Z. grandis* (7.1-4 K), *Z.* cf. *tenuinervis* (5.1-1 K; 7.1-74 K), *Zonalapollenites dampieri* (5.1-3 K).

Angiosperms

Acanthaceae (see also Mendonciaceae; 4.1-18 O/O–M): *Aphelandra* (6.1-18 Q), *Beloperone* (7.6-20 Q), *Bravaisia* (4.1-26 Pl, 39/40 Q; 7.6-25 Q), *Comocladia* (4.1-26 Pl), *Dicliptera* (7.6-20 Q), *Hygrophila* (5.1-20 M), *Justicia* (4.1-26 Pl; 6.1-18 Q), *J. californica* (4.1-28 Q), *Multiaerolites formosus* (4.1-22 Pl [*Justicia* type]; 7.1-100 K; 7.2-43 M), *Multimarginites vanderhammeni* (7.2-43 M, 50 M), *Stendandrium* (7.6-30 Q), *Trichanthera* (6.1-18 Q).

Aceraceae: *Acer* (6.1-11 Q).

Aexotoxicaceae: *Aex(o)toxicon* (7.6-12 Q), *Aexotoxicoxylon harambouri* (7.2-15 M).

Agavaceae (4.1-18 O/O–M): *Agave* (4.1-29, 30 Q; 6.1-11 Q), *A. deserti* (4.1-28 Q), *A. subsimplex* (4.1-28 Q).

Aizoaceae: *Mollugo* (6.1-18 Q).

Akaniaceae: *Akania americana* (7.1-25–27 Pa).

Alangiaceae: *Lanagiopollis eocaenica* (4.1-9 E; *Alangium*).

Alismataceae (7.2-39 Pl; 7.6-7 Q): *Echinodorus* (7.6-32, 33 Q), *Sagittaria* (4.1-18 O/O–M, 32 Q; 7.6-13 Q), *Sagittaria–Echinodorus* (7.6-20, 30 Q).

Amaranthaceae (see also Chenopodiaceae for chenoams = Chenopodiaceae–Amaranthaceae undifferentiated): *Alternanthera* (6.1-1 Q, 11 Q, 19 Q, 20 Q; 7.6-6, 8, 18, 20, 24, 25, 30, 31 Q), *Amaranthus* (4.1-28 Q; 5.1-23 Q; 7.6-8, 20 Q, *Amaranthus* type [chenoam]), *A. australis* (7.6-25 Q), *A. dubius* (7.6-25 Q), *Gomphrena* (7.6-13 [under Amaranthaceae], 25, 30, 31 Q), *Iresine* (4.1-26 Pl; 6.1-2 Q, 9 Q, 11 Q, 18 Q), *Orapollis* (7.2-10 M), *Tidestromia* (4.1-30 Q).

Amaryllidaceae: *Bomarea* (7.6-20 Q).

Anacardiaceae (4.1-18 O/O–M, 33, 34, 39/40 Q; 5.1-23 Q; 7.1-94 O–M; 7.6-13, 25, 30 Q): *Ailanthipites* (7.1-37 Pa; see also Other Angiosperms), *A.* cf. *marginatus* (7.1-50 O; 7.2-13 M;

Anacardiaceae?), *A.* cf. *nonprolatus* (7.2-13 M), *Anacardioxylon caracoli* (7.1-78c O–M; 7.2-35 O–M), *Anacardites americanus* (7.2-41, 44 M), *A. braziliensis* (7.2-46 Pl), *A. brittoni* (7.1-41 E), *A. lanceolatus* (4.1-24 M), *A. pichileufensis* (7.1-15, 41 E), *A. rioturbioensis* (?) (7.1-15 Pa/E), *A. spondiaeformis* (7.2-44 M), *Anacardium* (7.1-57 E; 7.2-39 Pl), *A. eocenicum* (7.1-75 E), *A. peruvianum* (7.1-69, 70, 72 E), *A.–Tapirira* (7.6-30 Q), *Astronium* (7.6-20, 30 Q), *A. argentinum* (7.1-41 E), cf. *Campnosperma* (6.1-2 E, 23 Q), *Colombicarpum biloculare* (Reid, 1933), *Comocladia intermedia* (4.1-17 O/O–M), *Cotinus coggygria* (6.1-15 Pl/Pl–Q), *Duvaua pliocenica* (7.2-25 Pl), *Haplorhus medranoensis* (4.1-17 O/O–M), *Lithraea–Schinus* (7.6-32 Q), *Loxopterygium laplayense* (7.2-30 M), *Metopium* (5.1-23 Q), *M. prenuntium* (5.1-17 M), *Pachycormus* (4.1-25 M), *Pistacia* (4.1-25 M), *P. marquezii* (4.1-17 O/O–M), *Pseudosmodingium mirandae* (4.1-Ramírez et al., 2000), *P. terrazasiae* (4.1-Ramírez et al., 2000), *Retitricolporites chubutensis* (7.1-19 K; Anacardiaceae?; see also Other Angiosperms), *R.* sp. A (7.1-31, 32 Pa), *Rhoipites* (7.2-45 M), *R.* cf. *minusculus* (7.1-31, 32 Pa; see also Other Angiosperms), *Rhoophyllum serratum* (7.1-15 O, 38 E), *Rhus* (4.1-17 O/O–M, 25 M, 29 Q; 6.1-15 Pl/Pl–Q; 7.1-57 E; 7.6-20 Q), *R. toxicodendroides* (4.1-17 O/O–M), *Schinopsis* (7.1-25–27 Pa, 57 E), *S. balansiformis* (7.1-41 E), *S.* (?) *dubia* (7.1-8 K; 7.2-5 M), *S. morongifolia* (7.1-41 E), *S. patagonica* (7.1-15 E; 7.2-19b M), *Schinus* (7.6-4, 6, 7 Q), *S. herbstii* (7.2-6 M), *S. molliformis* (7.1-41 E), *Spondias* (5.1-23 Q; 6.1-2 Q, 3 Q, 12 Q; 7.6-24, 25 Q), *S. lutea* (5.1-21, 22 Q), *S. mirifica* (7.2-46 Pl), *Striatricolporites angustinus* (7.1-86 E), *S. gamerroi* (7.1-51 O; 7.2-10, 13 M; see also Other Angiosperms), *Tapirira* (4.1-25 M; 7.6-25, 32 Q), *T. lanceolata* (7.2-28a, 30, 31, 33, 42, 44 M), *T. trinitiana* (7.2-44 M).

Annonaceae (6.1-17 Q, 18 Q): *Annona* (6.1-15 Pl/Pl–Q; 7.1-25–27 Pa), *A. carnavalii* (7.2-49 Pl), *A. cetera* (5.1-8 O), *A. coronelensis* (7.1-58 E; 7.2-19a M), *A. costaricana* (6.1-5 Pl), *A.* cf. *guppyi* (7.2-33, 40 M), *A. infestans* (7.1-41 E), *A. lamegoi* (7.2-49 Pl), *A. oliveirae* (7.2-49 Pl), *A. peruviana* (7.1-70, 72 E), *A. precochambensis* (7.1-15 E), *A. pseudoglabra* (5.1-8 O), *A. rioturbioensis* (7.1-15 E), *A. saraviana* (4.1-24 M; 7.2-42 M), cf. *A. speciosa* (7.1-15 E; 7.2-19a M), *A. winslowiana* (7.2-28a M), *Cymbopetalum* (6.1-10 M), *Foveomorphomonocolpites humbertoides* (7.1-81, 82 K; see Other Angiosperms), *Guatteria* (type; 6.1-20a Q), *G. culebrensis* (6.1-6 M; 7.2-28a M), *Longapertites brasiliensis* (7.1-86 E; Annonaceae type), *L. perforatus* (7.1-86 E; Annonaceae type), *Oxandra emygdiana* (7.2-49 Pl), *Proxapertites humbertoides* (7.1-85 Pa/E, *Malmea*), *P. tertiaria* (7.1-84 Pa; 7.2-43, 50 M), *Rollinia* (?) *patagonica* (7.1-8 K), *R. tertiaria* (7.2-46 Pl), *Xylopia aromatica* (5.1-23 Q).

Antherospermataceae (see Monimiaceae).

Apiaceae (see Umbelliferae).

Apocynaceae (6.1-18 Q; 7.6-13, 20, 25, 30 Q): *All(e)amanda carmensis* (4.1-24 M), *A. crassostipitata* (7.1-15, 41, 58 E; 7.2-19a M), *Apocynophyllum chilense* (7.1-58 E; 7.2-19a M; *Apocynophyllum*, see also Other Angiosperms), *A. mexicanum* (4.1-24 M), *A. potosianum* (7.2-23, 25 Pl), *A. pseudowillughbya* (5.1-8 O), *A. salvadorensis* (7.2-40 M), *A.* cf. *texensis* (7.1-89 E), *A. wilcoxense* (?) (5.1-8 O), *Aspidosperma collazoensis* (5.1-8 O), *Echites ettingshauseni* (7.2-44 M), *E. pseudostellaris* (5.1-8 O), *E. tertiaria* (7.1-41 E), *Forsteronia* (7.6-30 Q), *Haemadictyon tenuifolium* (7.1-58 E; 7.2-19a M), *Hancornia* (7.6-31 Q), *H. minor* (5.1-8 O), *H. pseudopubescens* (5.1-8 O), *Lacmellea* (6.1-14 Pl), *Landophia paraparaensis* (7.1-41 E), cf. *Macoubea* (7.2-39 Pl), *Malouetia* (6.1-18 Q), *Plumiera alia* (7.2-44 M), *P. articulatifolia* (7.1-41 E), *P. evidens* (5.1-8 O), *P. rubraformis* (7.2-46 Pl), *P. tertiaria* (7.2-30 M), *Psilastephanoporites herngreenii* (7.2-50 M), *Rau(v)wolfia* (5.1-10 O, 23 Q; 6.1-18 Q), *Reevesia* (4.1-18 O/O–M), *Rhabdadenia* (4.1-18 O/O–M), *Tabernaemontana* (6.1-18 Q), *Thevetia angustifolia* (7.1-58 E; 7.2-19a M).

Aquifoliaceae: *Aquifoliphyllum ilicioides* (7.1-98 E), *Gemmatricolpites subsphaericus* (7.1-31, 32, 37 Pa; see also Other Angiosperms), *Ilex* (4.1-18 O/O–M, 23, 25 M, 26 Pl, 31, 32 Q; 5.1-10 O, 23 Q; 6.1-2 E, 3 Q, 7–10 M, 13–15 Pl/Pl–Q, 16–18 Q, 20 Q, 23 Q; 7.1-94 O–M; 7.2-27 Pl; 7.6-16, 20, 21, 23, 28–33 Q), *I. arcinervis* (7.2-32 M, 36 Pl), *I. bahiana* (7.2-46 Pl), *I. subtilinervis* (7.1-58 E; 7.2-19a M), *Ilexpollenites* (4.1-8 K; 7.2-45, 50 M), *I. auriculoides* (4.1-10 E; *Ilex*), *I. clifdenensis* (7.1-45 E), *I. iliacus* (7.2-43 M), *I. margaritus* (7.2-43 M).

Araceae (7.6-32 Q): *Anthurium* (7.2-39 Pl), *Caladiosoma miocenica* (7.2-41, 44 M), *Ephedripites* (7.1-31, 32, 37 Pa; some smaller forms that are densely striate rather than polyplicate may represent Araceae of the *Spathiphyllum* type; see also Other Angiosperms), *E. renzonii* (7.2-50 M), *E. vanegensis* (7.1-84 Pa), *Monstera marginata* (7.1-98 E), *Spathiphyllum* (4.1-26 Pl), *Stenospermation columbiense* (7.2-28a, 32 M, 36 Pl); see also *Proxapertites operculatus* (Palmae, 7.1-84).

Araliaceae (6.1-2 E, 6 Q, 13 Q, 14 Q; 7.1-94 O–M; 7.6-25 Q): *Dendropanax* (5.1-10 O), *Didymopanax* (7.6-24, 29, 31, 32 Q), cf. *Oreopanax* (7.2-27 Pl), *O.* cf. *fulvum* (7.6-32 Q), *O. guinazui* (7.1-41 E), *Pseudopanax latetevirens* (7.6-9, 12 Q).

Arecaceae (see Palmae).

Aristolochiaceae (7.6-31 Q).

Asclepidaceae (7.6-20 Q): *Marsdenia macrophylla* (6.1-15 Pl), *Patrisia eocenica* (7.1-15 E; 7.2-19a M), *Polioexolobus molinae* (7.1-15 E), *P. prenuntius* (7.1-41 E).

Asteraceae (see also Compositae): Asteraceae high spine (4.1-29 Q; 6.1-1–3 Q, 6 Q, 9, 20a Q, 22 Q), Asteraceae low spine (4.1-29 Q).

Avicenniaceae: *Avicennia* (also Verbenaceae; 6.1-18 Q).

Balanophoraceae: *Scybalium* (7.6-20 Q).

Begoniaceae: *Begonia* (7.6-14, 32 Q).

Berberidaceae: *Berberis* (7.2-16 M; 7.6-2, 4, 7, 12 Q), *B. boweri* (7.1-38 E), *B. corymbosifolia* (7.1-41 early M or E), *Mahonia* (4.1-25 M).

Betulaceae (see also Corylaceae): *Alnipollenites trina* (4.1-8 K), *A. verus* (7.2-43 M), *Alnus* (4.1-26 Pl, 31–39/40 Q; 6.1-2 Q, 3 Q,

5 Q, 6 Q, 11 Q, 13–18 Q; 7.2-14 M; 7.6-7, 8, 13–18, 21–23, 33 Q), *A. jorullensis* (7.6-20 Q), *Betula* (4.1-18 O/O–M), *Carpinus* type (6.1-2 Q, 3 Q), *C. subtriangulata* (4.1-8 K), *Carpinus–Corylus–Ostrya* (4.1-31–34, 36 Q; 6.1-11 Q), *Trivestivulopollenites* (7.2-13 M).

Bignoniaceae (4.1-18 O/O–M, 37 Q; 6.1-15 Pl/Pl–Q; 7.6-30 Q): *Adenocalymma tertiaria* (7.1-15, 41 E), *Arrabidaea* (7.2-47 Pl; 7.6-30 Q), *A. patagonica* (7.2-19b M), *Bignonia gigantifolia* (7.1-15 E, 58 E; 7.2-19a M), *B. neogenia* (7.2-28b M), *B. pilchileufuana* (7.1-15 E, 41 undifferentiated), *B. tertiaria* (7.2-30, 34 M), *B. zulliana* (5.1-17 M), *Bignonites americanum* (7.2-28b M), *B. chalianus* (7.2-5 M), *B. ovatus* (7.2-19b M), *Bignonoides orbicularis* (4.1-24 M; *Bignonoides*, see also Other Angiosperms), *Crescentia cucurbitinoides* (4.1-24 M), cf. *Cydista* (7.6-20 Q), *Eccremocarpus longiflorus* (7.6-20 Q), *Jacaranda* (5.1-10 O), *J. coerulea* (5.1-23 Q), *J. potosiana* (7.2-23, 25 Pl), *J. tertiaria* (7.2-46, 47 Pl), *Margocolporites* (7.1-50 O; *Jacaranda*; see also Other Angiosperms), *Melloa* (?) *cuquensis* (7.2-41 M), *Paragonia–Arrabidaea* (6.1-2 E), *Tabebuia* (7.6-30 Q), *T. ipiformis* (7.1-15, 41 E), *Tecoma* (5.1-10 O; 7.1-57 E), *T. grandidentata* (7.2-32 M, 36 Pl), *T. serrata* (7.1-15, 58 E; 7.2-19a M).

Bixaceae: *Banara cuadrae* (7.2-19a M, see Flacourtiaceae), *Laetia transverso[i]nervis* (7.2-19a Ma, see Flacourtiaceae).

Bombacaceae (see also Sterculiaceae, Tiliaceae; 4.1-21 O/O–M, 34 Q; 6.1-2 Q, 11 Q, 12 Q, 13 P, 17 Q; 7.6-25 Q): *Aguiaria* (6.1-9, 10 M), *Bernoullia* (5.1-10 O; 6.1-10 M), Bombacaceae (cf. *Aguiaria* type; 4.1-21 M), *Bombacacidites* (4.1-18 O/O–M; 5.1-7a E; see also Other Angiosperms), *B. annae* (7.1-85 Pa–E), *B. araracuarensis* (7.2-50 M, *Ceiba*), *B. baculatus* (7.2-43, 50 M, *Pachira*), *B. baumfalki* (7.2-43, 50 M), *B. bellus* (7.1-91 E; 7.2-43, 50 M), *B. brevis* (7.1-85 Pa–E), *B. ciriloensis* (7.2-43 M), *B. claibornensis* (4.1-10 E), *B. fossureticulatus* (7.1-85 Pa–E), *B. foveoreticulatus* (7.1-85 Pa–E), *B. gonzalezii* (7.1-85 Pa–E), *B. grahamii* (7.1-85 Pa–E), *B. mirabilis* (5.1-4 E), *B. muinaneorum* (7.2-50 M, *Bombacopsis*), *B. nacimientoensis* (4.1-10 E; 7.1-85 Pa–E), *B. paulus* (4.1-9 E; possibly Sterculiaceae–Tiliaceae), *B. protofoveoreticulatus* (7.1-85 Pa–E), *B. psilatus* (7.1-85 Pa–E), *B. simplireticulatus* (7.1-85 Pa–E), *B. soleaformis* (7.1-85 Pa–E, 91 E), *B.* cf. *tilioides* (5.1-7 E), *B. zuatensis* (7.2-43 M), *B.* types 1, 2 (5.1-7 E), *Bombaciphyllum opacum* (7.1-58 E; 7.2-19a M), *Bombax* (4.1-22 M; 5.1-10 O; 6.1-3 Q; 7.1-66 E–O), *B. aramariensis* (7.2-46 Pl), *B. firmifolium* (7.1-15, 58 E; 7.2-19a M), *B. playense* (7.2-19a M), *B. prebarrigon* (7.2-44 M), *B. retusifolium* (7.2-30, 31 M), tipo *Bombax* (5.1-23 Q), *Catopsis* (6.1-18 Q), *Catostemma* (5.1-10 O, 23 Q; 7.1-94 O, M), *Cavanillesia* (6.1-18 Q; 7.2-27 Pl; 7.6-30 Q), *Ceiba* (6.1-9, 10 M, 11 Q, 13 Q, 14 Q, 15 Pl/Pl–Q, 18 Q), *Chorisia* (7.6-31 Q), *Eriotheca* (7.6-31 Q), *Gyranthera darienensis* type (6.1-18 Q), *Jandufouria seamrogiformis* (7.2-43, 50 M, *Catostemma*; *Jandufouria*, see also Other Angiosperms), *Ochroma* (6.1-18 Q), *Pachira* (4.1-20 O/O–M; 6.1-18 Q), *Pseudobombax* (6.1-9, 10 M, 18 Q), *Quararibea* (6.1-18 Q), *Retistephanocolpites angeli* (7.1-86 E, *Catostemma*; see also Other Angiosperms), *Retistephanoporites crassiannulatus* (7.2-43 M; 7.2-50 M, *Quararibea*), *Retitricolpites lorentae* (7.2-50 M), *Retitricolporites annae* (7.1-84 Pa), *Zizyphus* (7.1-15 E).

Boraginaceae (4.1-18 O/O–M, 33 Q; 7.6-20 Q): *Amsinckia tessellata* (4.1-28 Q), *Cordia* (4.1-39/40 Q), *C. alliodora* (6.1-18 Q), *C. curassavica* (7.6-30 Q), *C. galeottiana* (5.1-22 Q), *C. lantana* (7.6-20, 30 Q), *C. pulchra* (7.1-58 E; 7.2-19a M, Cordiaceae), *C. sebestena* (5.1-22 Q), *C. vera* (7.1-77 E), *Cryptantha barbigera* (4.1-28 Q), *C. decipiens* (4.1-28 Q), *C. diffusa* (7.6-11 Q), *C. hispida* (7.6-11 Q), *C. limensis* (7.6-11 Q), *C. maritima* (4.1-28 Q), *C. phaceloides* (7.6-11 Q), *C. pterocarya* (4.1-28 Q), *C. vera* (7.1-77 E), *Heliotropium* (5.1-23 Q; 7.6-7 Q), *Lithospermites glabrum* (7.1-70 E), *Moritzia* (7.6-20 Q), *Pectocarya dimorpha* (7.6-11 Q), *Tiquilia atacamensis* (7.6-11 Q), *Tournefortia* (4.1-26 Pl; 5.1-10 O; 7.6-20 Q).

Brassicaceae–Cruciferae (see Cruciferae; 4.1-29 Q).

Bromeliaceae (see also Liliaceae, possibly some *Liliacidites*; 5.1-23 Q; 7.6-30 Q): *Ananas* (7.6-31 Q), *Bromelia* (7.6-30 Q), cf. *Catopsis* (7.2-39 Pl), *Dyckia* (7.6-31 Q), *Karatophyllum bromeloides* (text, Costa Rica), *Puya* (6.1-16 Q; 7.6-17, 20 Q), *Tillandsia* (4.1-23 M; 6.1-2 E).

Brunelliaceae: *Brunellia* (5.1-10 O).

Burseraceae (6.1-2 Q, 8 Q): *Bursera* (4.1-18 O/O–M, 25 M, 26 Pl, 29, 32, 33, 37, 39/40 Q; 5.1-10 O, 24 Q; 6.1-1 Q, 3 Q, 5 Q, 6 Q, 9, 14 Q, 10 M, 18 Q, 20 Q; 7.6-24, 25 Q), *B. microphylla* (4.1-28 Q), *B. simaruba* (5.1-23 Q), *Burserites fayettensis* (7.1-89 E), *B. venezueleana* (7.2-40 M), *Icica pichileufuana* (7.1-41 E), *I. tertiaria* (7.2-19b M), *Paraprotium* (7.2-39 Pl), *Protium* (4.1-26 Pl; 6.1-2 E, 23 Q; 7.6-25, 30 Q), *P. cubense* (5.1-23 Q), *Tetragastris* (6.1-2 E).

Buxaceae (see Simmondsiaceae): *Styloceras laurifolium* (7.6-20 Q), *S. tertiarium* (7.1-41 E).

Cabombaceae: *Cabomba* (6.1-10 M).

Cactaceae (4.1-39/40 Q): *Carnegiea gigantea* (4.1-28 Q), cf. *Cereus* (7.6-7, 30 Q), *Echinocereus* (4.1-28 Q; 6.1-11 Q), *Echinopsis atacamensis* (7.6-11 Q), *Ferocactus cylindraceus* (4.1-28 Q), *Lophocereus schottii* (4.1-28 Q), *Mammillaria grahamii* (4.1-28 Q), *M. microcarpa* (4.1-28 Q), *Opuntia arbuscula* (4.1-28 Q), *O. bigelovii* (4.1-28 Q), *O. camachoi* (7.6-11 Q), *O. fulgida* (4.1-28 Q), *O. ignescens* (7.6-11 Q), *O. sphaerica* (7.6-11 Q), *O. kunzei* (4.1-28 Q), *O. ramosissima* (4.1-28 Q), *Oreocereus* (7.6-11 Q), *Pachycereus pringeli* (4.1-28 Q), cf. *Preskia* (7.2-27 Pl).

Callitrichaceae: *Callitriche* (7.2-39 Pl).

Calyceraceae: *Calycera* (7.6-6 Q).

Campanulaceae: Campanulaceae cf. *Rhizocephalum* (7.6-13 Q), *Lobelia tenera* type (7.6-20 Q), *Lysipomia* (7.6-20 Q), *Rhizocephalum* (7.6-23 Q), R. *candollei* (7.6-20 Q).

Canellaceae: *Canella winterianafolia* (7.2-46 Pl), *Pleodendron* (5.1-10 O).

Cannaceae: *Canna* or *Heliconia* (Heliconiaceae) (7.1-88 E).

Capparidaceae: *Capparis multinervis* (7.2-21 M, 23, 25 Pl), *C. prejamaicensis* (5.1-17 M), *C. verrucosafolia* (7.2-30 M), *Cleome* (6.1-16 Q; 7.6-20 Q).

Caprifoliaceae (4.1-30, 37 Q): *Symphoricarpos microphyllus* (4.1-27 Q), *Viburnum* (6.1-16 Q; 7.6-20 Q).

Caryocaraceae: *Caryocar* (7.6-30 Q).

Caryophyllaceae (4.1-18 O/O–M, 29, 33, 37, 39/40 Q; 6.1-3 Q, 9 Q, 11 Q, 16 Q, 20 Q; 7.6-2–4, 7, 9, 12, 13, 15, 20–23, 31, 32 Q): *Arenaria* type (7.6-8, 20 Q), *Drymaria villosa* type (7.6-20 Q), *Spergularia* (7.6-11 Q), *S.* type (7.6-6 Q).

Casuarinaceae: *Cassuarina* (7.1-25–27 Pa), *C. patagonica* (7.2-3 M), *Casuarinidites coenozoicus* (7.1-56 Pa), *Haloragacidites harrisii* (7.2-13 M, Casuarinaceae, Myricaceae).

Cecropiaceae (see Urticaceae).

Celastraceae (6.1-11 Q): *Celastris simplex* (5.1-17 M), *Celastrophyllum elaeodendriforme* (7.1-41 E), *C. fraunhoferifolium* (7.1-41 E), *Gyminda latifolioides* (7.2-46 Pl), *Hippocratea* (6.1-17 Q; 7.6-30 Q), *H. volubilis* (6.1-18 Q), *Hippocratea*, *Pristimera* (7.2-39 Pl), *Maytenus* (7.6-2, 7, 9, 12 Q), *M. anzoateguiensis* (7.2-42 M), *M. araucensis* (7.1-58 E; 7.2-19a M), *M. dasycladoides* (7.2-46 Pl), *M. ellipticus* (7.1-41 E), *M. latifolioides* (7.1-41 E; 7.2-19b M), *M. magnoliaefolia* (7.1-58 E; 7.2-19a M), *M. trinitense* (7.2-42, 44 M), *Plenckia* (7.6-30 Q), *Salacia* (7.6-31 Q), *Schaefferia* (4.1-25 M), *Tontelea* (6.1-2 E), *Villaresia* (7.6-31 Q).

Centrolepidaceae: *Gaimardia australis* (7.6-12 Q).

Ceratophyllaceae: *Ceratophyllum* (4.1-36 Q), *C. demersum* (6.1-15 Pl/Pl–Q), cf. *C. llerenae* (6.1-15 Pl/Pl–Q).

Chenopodiaceae (including chenoams = Chenopodiaceae–Amaranthaceae undifferentiated; 4.1-18 O/O–M, 26 Pl, 29, 30, 31–39/40 Q; 5.1-20 M, 23, 24 Q; 6.1-1–3 Q, 6 Q, 7 M, 7 Q, 9, 14 Q, 15 Pl/Pl–Q, 17–19 Q, 22 Q; 7.1-19 K [?]; 7.6-2–8, 12, 13, 15, 17, 20, 24, 32 Q): *Atriplex imbricata* (7.6-11 Q), *Chenopodipollis* (7.1-51 O; see also Other Angiosperms), *C. chenopodiaceoides* (7.2-8, 10, 13 M; see also Other Angiosperms), *Psilaperiporites* (7.1-91 E), *P. minimus* (7.2-43, 50 M; see also Other Angiosperms), *P. robustus* (7.2-43 M), *Sarcobatus* (4.1-29, 30 Q).

Chloranthaceae: *Clavainaperturites microclavatus* (7.2-50 M), *Clavatipollenites* (7.1-51 O; see also Other Angiosperms), *Hedyosmum* (4.1-22 Q, 26 Pl, 38 Q; 6.1-2 Q, 5 Q, 6 Q, 11 Q, 13 Q, 14 Q, 16 Q, 18 Q, 19 Q; 7.6-13–17, 20–23, 30, 31 Q), *H. brasiliense* (7.6-32 Q), *Inaperturopollenites crisopolensis* (7.1-74 K, Chloranthaceae?).

Chrysobalanaceae (6.1-20a Q; 7.2-39 Pl): *Chrysobalanus icaco* (5.1-21 Q, 22 Q), *Licania arborea* (6.1-18 Q), *Moquilea mexicana* (4.1-24 M; see also Rosaceae), *Parinari* (7.2-39 Pl), *Rugutricolporites arcus* (7.2-50 M).

Clethraceae (4.1-18 O/O–M): *Clethra* (6.1-16 Q; 7.6-13, 14, 20, 32, 33 Q).

Clusiaceae (see Guttiferae).

Cochlospermaceae: *Cochlospermum* (7.1-25–27 Pa), *C. previtifolium* (7.1-41 E).

Combretaceae: *Bredelipollis* (7.1-51 O, *Combretum–Terminalia*), cf. *Bucida* (6.1-10 M), *B. buceras* (6.1-15 Pl/Pl–Q), *B. sanchezensis* (5.1-15 M), *B.–Conocarpus* (5.1-23 Q), Combretaceae–Melastomataceae (6.1-11 Q), *Combretum* (6.1-18 Q; 7.6-30, 31 Q), *C. fonsecanensis* (7.2-47 Pl), *C. incertum* (7.2-44 M), *C. jacquinifolia* (7.2-42 M), *C. oblongifolium* (7.1-58 E; 7.2-19a M), *C.* cf. *petraflumensis* (7.1-88 E), *C. pseudojacquinii* (5.1-8 O), *Combretum–Terminalia* (4.1-26 Pl; 6.1-2 E, 3 Q, 7 M, 8 Q, 10 M/M–Pl, 12 Q), *Conocarpus* (5.1-21 Q; 6.1-18 Q), *C. erectus* (7.6-26 Q), *Laguncularia* (4.1-26 Pl), *L. racemosafolia* (5.1-17 M), *Nothopollenites* (7.1-34, 35 Pa), *Terminalia antiqua* (7.2-22 M, 23, 25 Pl), *T. maxima* (7.2-47 Pl), *T.* cf. *phaeocarpoides* (7.1-88 E), *T. singewaldi* (7.2-23–25 Pl), *T. trinitense* (7.2-44 M), *Terminalioxylon naranjo* (7.1-78c O–M; 7.2-35 O–M), *T. porosum* (7.2-35 O–M).

Compositae (see also Asteraceae; 4.1-18 O/O–M, 26 Pl, 30–39/40 Q; 5.1-20 M, 24 Q; 6.1-7, 8, 11 M/M–Pl, 12, 13, 15 Pl/Pl–Q; 7.1-61 E [Compositae type, age uncertain], 63 O [Compositae type]; 7.2-27, 39 Pl; 7.6-5, 6, 9, 13, 15, 17, 18, 20–23, 25, 30, 31 Q): *Ambrosia* (4.1-22 Pl, 29, 32, 36, 37, 39/40 Q; 5.1-23, 24 Q; 6.1-1–3 Q, 11 Q; 7.6-15, 17, 18, 24, 32 Q), *A. artemisioides* (7.6-11 Q), *A. chenopodiifolia* (4.1-28 Q), *A. deltoidea* (4.1-28 Q), *A. dumosa* (4.1-28 Q), *A.–Xanthium* (7.6-6 Q), *Artemisia* (4.1-22 Pl, 29, 30, 32, 34, 36 Q; 7.6-8, 20 Q), *Baccharis* (4.1-25 M; 7.6-32, 33 Q), *B. boliviensis* (7.6-11 Q), *B. tola* (7.6-11 Q), *B.* type (7.6-8 Q), *Bebbia* (4.1-28 Q), *Benettia grosse-serrata* (7.2-19a M), *Bidens* aff. *pilosa* (7.6-11 Q), *B.* aff. *pseudocosmos* (7.6-11 Q), *Brickellia* (4.1-25 M), *B. atractyloides* (4.1-28 Q), *B. coulteri* (4.1-28 Q), *Carduus* type (7.6-6 Q), *Chaenactis* cf. *stevioides* (4.1-28 Q), *Chrysothamnus teretifolius* (4.1-28 Q), *Chuquiraga atacamensis* (7.6-11 Q), *Cirsium* (4.1-29 Q), Compositae–Asteroideae (7.6-32 Q), Compositae–Chichorioideae (7.6-4, 6 Q), Compositae–Liguliflorae (4.1-29 Q; 7.6-2, 7, 12, 20, 32 Q), Compositae–Mutisieae (6.1-10 M; 7.6-4 Q), Compositae–Tubuliflorae (7.6-2–4, 7, 12, 16, 20, 24, 29, 32 Q), *Compositoipollenites* (7.2-45 M), *C.* aff. *tarragoensis* (7.1-51 O; oldest for Patagonia), cf. *Conyza deserticola* (7.6-11 Q), *Cypselites potosianus* (7.2-23, 25 Pl), *Dicoria canescens* (4.1-28 Q), *Diplostephium meyenii* (7.6-11 Q), *Echitricolporites maristellae* (7.2-43 M), *E. mcneillyi* (7.2-43 M), *E. spinosus* (7.2-43 M), *Encelia farinosa* (4.1-28 Q), *E.* type (7.6-8 Q), *Fenestrites longispinosus* (7.2-43 M), *F. spinosus* (7.2-43 M), *Franseria* type (7.6-8 Q), *Gnaphalium* type (7.6-8 Q), *Helianthus* (4.1-22 Pl, M), *Helogyne macrogyne* (7.6-11 Q), *Hofmeisteria fasciculata* (4.1-28 Q), *H. pluriseta* (4.1-28 Q), *Hymenoclea salsola* (4.1-28 Q), *Iva* type (6.1-11 Q), *Jungia* type (7.6-33 Q), *Loricaria* (7.6-17, 20 Q), *Multisiapollis viteauensis* (7.1-52 O; 7.2-8, 10 M, *Mutisia*, see Other Angiosperms), *Mutisia* (7.6-8, 20 Q), *Nassauvia* (7.6-4, 5 Q), *Pacourina edulis* (6.1-18 Q), *Pamphalea* (7.6-32, 33 Q), *Parastrephia quadrangularis* (7.6-11 Q), *Pectis papposa* (4.1-28 Q), *Perezia* (7.6-8, 12 Q), *Perityle emoryi* (4.1-28 Q), *Peucephyllum schottii* (4.1-28 Q), *Pleurocoronis laphamioides* (4.1-28 Q), *Porophyllum gracile* (4.1-28 Q), *Rafinesquia neomexicana* (4.1-28 Q), *Schkuhria multiflora* (7.6-11 Q), *Senecio* (4.1-27 Q; 6.1-12 Q; 7.6-8, 32, 33 Q), *S.* aff. *atacamensis* (7.6-11 Q), *Tagetes multiflora* (7.6-11 Q), *Trixis* (7.6-32 Q), *T. californica* (4.1-28 Q), *Tubulifloridites* (7.1-51 O), *T. antipodica* (7.1-52 O; 7.2-8, 10, 13 M), *T. simplis* (7.2-13 M), *T. viteauensis* (7.1-52 O; 7.2-13 M), *T.* sp. (7.2-13 M), *Urmenetea*

atacamensis (7.6-11 Q), *Vernonia* (7.6-32 Q), *Viguiera* cf. *deltoidea* (4.1-28 Q), *V. laciniata* (4.1-28 Q).

Connariaceae: *Connarus* (7.2-39 Pl), *C. carmenensis* (4.1-24 M), cf. *Rourea* (6.1-7 M).

Convolvulaceae (4.1-37 Q; 7.6-7 Q): *Bonamia* (7.6-32 Q), *Evolvulus* (5.1-23 Q; 7.6-20 Q), *Ipomoea* (4.1-37 Q; 5.1-23 Q; 6.1-18 Q; 7.6-25 Q), *Maripa* (6.1-18 Q), *Merremia* (6.1-18 Q; 7.6-20 Q), *Perfotricolpites digitatus* (7.1-85 Pa–E; 7.2-50 M, *Merremia*; 7.2-43 M; see also Other Angiosperms).

Cordiaceae (see Boraginaceae).

Coriaceae: *Coriaria ruscifolia* (7.6-20 Q).

Corylaceae: *Corylus* (4.1-18 O/O–M).

Crassulaceae: *Echeveria* (7.6-20 Q).

Crossosomataceae (see Rosaceae).

Cruciferae (see also Brassicaceae–Cruciferae; 4.1-33 Q; 6.1-11 Q, 16 Q; 7.6-4, 6–8, 13 Q): *Draba* (7.6-20 Q), *D. cuneifolia* (4.1-28 Q), *D. hammenii* (7.6-20 Q), *Lepidium* (7.6-11, 20 Q), *L. lasiocarpum* (4.1-28 Q), *Lyrocarpa coulteri* (4.1-28 Q), *Retitricolpites* (7.2-45 M), *Sisymbrium philippianum* (7.6-11 Q), *Tricolpites* sp. 1 (7.2-13 M).

Ctenolophonaceae: *Ctenolophonidites cruciatus* (7.1-85 Pa–E, Ctenolophonaceae?).

Cucurbitaceae (7.6-25 Q): *Ceratosanthes* (7.6-31 Q), cf. *Cionosicys* (6.1-10 M), *Cucurbites compressus* (7.1-70 E), *Sechium* (6.1-18 Q).

Cunoniaceae (7.6-31 Q): *Caldcluvia* (7.2-16 M), *Lamanonia* cf. *speciosa* (7.6-32, 33 Q), *Rhoipites baculatus* (7.1-29 Pa; see also Other Angiosperms), *R. minusculus* (7.1-29 Pa; see also Other Angiosperms), *Weinmannia* (6.1-11 Q, 16 Q; 7.2-16 M; 7.6-15, 16, 20, 23, 32, 33 Q), *W. brittonii* (7.2-21 M, 23, 25 Pl), *W. potosina* (7.2-23, 25 Pl), *W. trichosperma* (7.6-9, 12, 13, 17 Q), *Weinmannioxylon multiperforatum* (7.1-24 Pa), *W. pluriradiatum* (7.1-24 Pa).

Cupuliferoidae (Fagales, fagaceous; 6.1-8 Q).

Cyclanthaceae: cf. *Asplundia* (7.2-39 Pl), cf. *Cyclanthus* (7.2-39 Pl), cf. *Evodianthus* (7.2-39 Pl), *Thoracocarpus* (7.2-39 Pl).

Cyperaceae (4.1-22 Q, 26 Pl, 29, 30–33, 35, 36, 38, 39/40 Q; 5.1-23, 24 Q; 6.1-1–3 Q, 6 Q, 8 Q, 10–23 Q, 11, 12, 15 M/M–Pl; 7.6-2–4, 6–8, 12, 13, 15–18, 20–25, 29, 31–33 Q): *Carex* (7.2-39 Pl), *Cladium* (5.1-24 Q), *C. jamaicense* (5.1-23 Q), *Cyperaceaepollis* (7.2-50 M), *C. neogenicus* (7.1-49, 52 O; 7.2-8, 10, 13, 43 M), *Cyperus* (5.1-23 Q), *C.–Kyllinga* (6.1-20a Q), *Dichromena* (4.1-25 M), *Eleocharis* (7.2-39 Pl), *Scirpus* (7.2-39 Pl; 7.6-17 Q), *Scleria wolfi* (7.2-30, 31 M), *Tetroncium magellanicum* (7.6-2, 3 Q).

Cyrilliaceae: *Cyrilla* (6.1-23 Q), *C. racemiflora* (5.1-23 Q), *Cyrillaceaepollenites* (7.2-45 M).

Dichapetalaceae: *Dichapetalum* (4.1-26 Pl).

Dilleniaceae: *Curatella* (7.6-30, 31 Q), *Doliocarpus* (6.1-7 M), *D. oblongifolia* (7.1-58 E; 7.2-19a M), *D.* (?) *serrulata* (7.1-58 E; 7.2-19a M), *Empedoclea repando-serrata* (7.1-58 E; 7.2-19a M), *Tetracera belensis* (7.1-70 E), *T. elliptica* (7.1-58 E; 7.2-19a M), *T. patagonica* (7.1-41 E; 7.2-19b M), *T. rhamnoides* (7.1-15, 58 E; 7.2-19a M), *T. tertiaria* (7.2-28b, 30 M).

Dioscoreaceae: *Dioscorea* (7.2-16, 33 M), cf. *Dioscorea–Rajania* (6.1-7 M), *Rajania* (4.1-26 Pl).

Droseraceae: *Drosera* (4.1-18 O/O–M; 7.6-30, 31 Q).

Ebenaceae: *Diospyros* (4.1-25 M), *D. macdonaldi* (6.1-6 M).

Elaeocarpaceae: *Elaeocarpoxylon sloaneoides* (7.1-24 Pa), *Muntingiophyllum calaburoides* (7.2-36 Pl), *Vallea* (7.6-13, 14, 20 Q), *V. prepubescens* (7.2-28b M).

Elatinaceae: *Elatine* (7.2-39 Pl).

Empetraceae: *Empetrum* (7.6-4, 7, 12 Q), *E. rubrum* (7.6-2, 12 Q), *Empetrum*–Ericaceae (7.6-3, 9, 12–17, 20–23, 30–32 Q), *Ericipites microtectatum* (7.1-30 Pa; see also Other Angiosperms), *E. scabratus* (7.1-30 Pa).

Epacridaceae: *Lebetanthus myrsinites* (7.6-12 Q).

Eremolepidaceae (see Santalaceae).

Ericaceae (see also Empetraceae; 4.1-21 O/O–M, 33, 34 Q; 5.1-23 Q; 6.1-10 M, 13 Pl, 15–18 Q; 7.2-27 Pl): *Arbutus* (4.1-27 Q), *Arctostaphylos* (4.1-25 M, 29 Q), *Comarostaphylis* (4.1-25 M), *Ericipites* (7.1-80 K; 7.2-43 M; see also Other Angiosperms), *E. annulatus* (7.1-86 E), *Gaultheria* (7.1-57 E), *G. ulei* (7.6-32 Q), *Gaylussacia ovata* (7.2-25 Pl), *G. tertiaria* (7.2-21 M, 23, 25 Pl), *Vaccinium pontzuelum* (7.2-24, 25 Pl).

Eriocaulaceae (6.1-16 Q): *Eriocaulon* (7.6-30 Q), *E.–Paepalanthus* (7.6-20, 32, 33 Q).

Erythroxylaceae: *Erythroxylon* (7.6-30 Q), *E. cuneifolioides* (7.1-41 E; 7.2-19b M), *E. reichei* (7.1-58 E).

Escalloniaceae: *Escallonia* (7.6-17, 23 Q), *Escallonioxylon palaeo-argutum* (7.1-54 K, *Escallonia*).

Eucommiaceae: *Eucommia* (4.1-18 O/O–M), *E. constans* (4.1-15 O/O–M).

Eucryphiaceae: *Eucryphia tertiaria* (7.1-41 E).

Euphorbiaceae (4.1-30, 33, 34, 37 Q; 5.1-24 Q; 6.1-2 Q, 11 Q, 16 Q; 7.6-4, 7, 30, 31 Q): *Acalypha* (4.1-25 M, 29, 39/40 Q; 6.1-1 Q, 2 Q, 9–11 Q, 17 Q, 18 Q, 21 Q, 22 Q; 7.6-13–15, 17, 18, 20, 24, 30, 32 Q), *Alchornea* (4.1-26 Pl; 5.1-10 O, 20 M, 24 Q; 6.1-2 Q, 5 Q, 6 Q, 7–10 M, 11 Q, 13 Pl, 14 Pl/Q, 16–18 Q, 22 Q; 7.6-13–17, 20, 21, 28–30, 32, 33 Q), *A. swartzi* (7.2-30 M), *Aleurites* (?) *platanoides* (7.1-58 E), *Argythamnia* cf. *lanceolata* (4.1-28 Q), *A.* cf. *neomexicana* (4.1-28 Q), *A. serrata* (4.1-28 Q), cf. *Bernardia* (4.1-26 Pl), *Bridelioxylon americanum* (7.1-24 Pa), *Caperonia palustris* (5.1-23 Q), *Chamaesyce* (7.6-30 Q), *Cnidoscolus* (7.6-30 Q), *Croton* (7.6-18, 20, 32 Q), *C. bogotense* (*C. bototanus*) type (7.6-20 Q), Euphorbiaceae–Crotonoid (6.1-18 Q), *Crototricolpites annemariae* (7.2-50 M), *Dalechampia* (7.6-20 Q), *Ditaxis lanceolata* (4.1-28 Q), *Drypetes elliptica* (4.1-24 M), *D. laterifloraforma* (5.1-17 M), *Euphorbia* (4.1-18 O/O–M, 25 M;

7.2-22 M, 23, 25 Pl; 7.6-11, 32 Q), *E. misera* (4.1-28 Q), *E. pediculifera* (4.1-28 Q), *E.* cf. *polycarpa* (4.1-28 Q), cf. *Glycydendron* (6.1-10, 13 Pl, 18 Q), *Hieronymia* (6.1-18 Q), *H. lehmanni* (6.1-5 Pl, 6 M; 7.2-31 M), *Homalanthus prenutans* (7.2-47 Pl), *Hura* (6.1-19 Q), *Jatropha* (6.1-10 M; 7.6-30 Q), *J.* cf. *cuneata* (4.1-28 Q), *J. tertiaria* (7.1-70 E), *Mabea* (6.1-18 Q; 7.6-30 Q), *Mallotus* (?) *platanoides* (7.2-19a M), *Malvacipollis spinulosa* (7.2-43 M), *M. subtilis* (7.2-10 M), *Manihot* (6.1-18 Q), *Maprounea* (7.6-31 Q), *Nyssapollenites endobalteus* (7.1-51, 52 O), *Omphales[a] filiciformis* (7.1-15, 58 E; 7.2-19a M), *O. flaviana* (7.1-15 E), *O. patagonica* (7.1-41 E), *Pera* (7.6-25, 32 Q), *Phyllanthus* (6.1-18 Q; 7.6-18, 32 Q), *Psilatricolporites* (7.2-45 M), *P. operculatus* (7.1-49, 52 O, 66 E–O, 91 E, 94 O–M; 7.2-43, 50 M, *Alchornea*; see also Other Angiosperms), *P. optimus* (7.1-86 E, *Alchornea*), *Ranunculacidites operculatus* (7.1-85 Pa–E, *Alchornea*), *Retitrescolpites* (?) *irregularis* (7.1-85 Pa–E), *Retitricolporites irregularis* (7.1-91 E; 7.2-43, 50 M, *Amanoa*; see also Other Angiosperms), *R. kaarsii* (7.2-50 M, *Dalechampia*), *Sapium* (4.1-26 Pl; 6.1-2 Q, 7 M, 14 Q, 16 Q, 18 Q; 7.6-20, 30 Q), *Sebastiania* (6.1-11 Q; 7.6-30 Q), *S. brasiliensis* (7.6-32 Q), *S. commersoniana* (7.6-32 Q), *S.* cf. *schottiana* (7.6-32 Q), cf. *Stillingia* (4.1-26 Pl; 6.1-10 M), *Tetraplandra longifolia* (7.1-58 E; 7.2-19a M), *Tetrorchidium* (4.1-26 Pl; 5.1-10 O; 6.1-7 M; 7.2-27 Pl), *T. rubrivenium* (7.6-32 Q), cf. *Tithymalus* (4.1-26 Pl).

Fabaceae (see Leguminosae).

Fagaceae (see also Cupuliferoidae; 7.2-8 M; for revision of *Nothofagus–Nothofagidites* fossil pollen types, see Dettmann et al., 1990): *Castanea* (4.1-18 O/O–M), *Cupuliferoidaepollenites* (7.2-45 M; see also Other Angiosperms), *Dryophyllum australis* (7.1-15 E, 28 Pa), Fagaceae undet. (7.1-15 Pa), *Fagophyllum duseni* (7.1-15 E, 28 Pa), *Fagus* ([South American = *Nothofagus*?] 4.1-32, 33 Q; 5.1-10 O [?]), *F.* [?] *dicksoni* (7.1-15, 38 E), *F. integrifolia* (7.1-38 E), *F. magelhaenica* (7.2-19a M), *F. morenoi* (7.1-15 E, Q), *F. obscura* (7.1-15 E, O), *F. subferruginea* (7.1-15 Pa, E, 38 E; 7.2-14 M), *Laurinoxylon uniseriatum* (7.1-54 K, Fagaceae?), *Nothofagidites* (7.1-55 K, 63 O), *N. acromegacanthus* (7.1-13 K, 46 E, 49, 51, 52 O; 7.2-10 M), *N. americanus* (7.1-49, 51, 52 O), *N.* cf. *asperus* (7.1-13 K, 43 E), *N. brachispinulosa* (7.1-43 E), *N. cincta* (7.1-43, 61 E), *N. cranwellae* (7.1-13 K, 43 E), *N. deminuta* (7.1-43 E), *N. dorotensis* (7.1-13 K, 46 E, 49, 51, 52 O; 7.2-13 M), *N. flemingii* (7.1-49, 51, 52 O), *N. fortispinulosus* (7.1-13 K, 43 E), *N. fuegiensis* (7.1-13 K), *N. huertasii* (7.1-85 Pa–E), *N. hystricosphaeroides* (7.1-13 K), *N.* cf. *incrassatus* (7.1-50 O), *N. kaitangatus* (7.1-13 K), *N. mensiesii* group (7.1-61 E), *N. micromarginata[us]* (7.1-43 E, 50 O), *N. nana* (7.1-43 E), *N. paucispinosus* (7.1-13 K), *N. rocaensis* (7.1-13 K), *N. saraensis* (7.1-13 K, 43, 46 E, 49–52 O; 7.2-10, 13 M), *N. suggatei* (7.1-13 K, 47 E), *N. tehuelchesii* (7.1-46 E, 49, 51, 52 O), *N.* cf. *visserensis* (7.1-13 K, 50 O), *N.* cf. *waipawensis* (7.1-13 K), *Nothofagoxylon antarcticum* (7.1-54 K), *N. ohzuanum* (7.1-54 K), *N. pseudoobliqum* (7.1-54 K), *N. sclarariforme* (7.1-54 K), *Nothofagus* (4.1-11 E, O/O–M; 7.6-2–4, 7 Q), *N. australis* (7.1-15 E), *N. brassii* group (7.1-60 E), *N. crenulata* (7.1-15 O; 7.2-14 M), *N. densinervosa* (7.1-15, 62 E), *N. dombeyi* (7.6-9, 12, 20 Q), *N. elongata* (7.1-15 E, O, 38 E), *N. fusca* group (7.1-60 E), *N. gonzalezii* (7.2-16 M), *N. lanceolata* (7.1-15 E, O; 7.2-14 M), *N. magellanica* (7.1-15 E), *N. obliqua* type (7.6-12 Q), *N. pulchra* (7.1-15 O), *N. serrulata* (7.1-15 E, O), *N. simplicidens* (7.1-15 E), *N. variabilis* (7.1-38 E; forma *microphylla* 7.1-15 Pa, E; forma *oblonga* 7.1-15 E, O), *Polycolpites* (7.2-45 M), *Quercus* (4.1-18 O/O–M, 22 Q, Pl, 25 M, 26 Pl, 29–39/40 Q; 6.1-1–3 Q, 5, 8 Q, 10, 11 M, 11–14 Q, 15 Pl/Pl–Q, 16 Q, 17 Q, 19 Q, 20 Q; 7.6-20 Q), *Q.* [?] *angustiloba* (7.1-15 E), *Q. aurita* (?) (5.1-3 K), *Q.* cf. *crassifolia* (6.1-15 Pl/Pl–Q), *Q. hahnii* (4.1-27 Q), *Q. hartwegi* (4.1-27 Q), *Q. laeta* (4.1-27 Q), *Q. laurina* (4.1-27 Q), *Q.* [?] *primordialis* (7.1-8 K), *Q. repanda* (4.1-27 Q), *Q. rugosa* (4.1-27 Q), *Q. rugulosa* (4.1-27 Q).

Flacourtiaceae (6.1-2 Q): *Azara* (7.1-57 E), *A. celastriniforma* (7.1-41 E), *A. tertiaria* (7.1-41 E), *Banara cuadrae* (7.1-41, 58 E; 7.2-19a M, see Bixaceae), *B. prehernandiensis* (7.1-41 E; 7.2-19b M), *Banara–Xylosma* (7.6-32 Q), *Banaraphyllum ovatum* (7.1-28 Pa), *Casearia* (4.1-26 Pl; 5.1-10 O, 23 Q; 6.1-2 E, 7 M/M–Pl), *C. oliganthoides* (7.1-58 E; 7.2-19a M), *C. patagonica* (7.1-15, 41 E), *C. piparoides* (7.1-58 E; 7.2-19a M), *C. serrata* (7.1-98 E), *C. spinuloso(a)-serrata* (7.1-15, 58 E; 7.2-19a M), *Laetia* (4.1-26 Pl), *L. transversinervis* (7.1-58 E; 7.2-19a M), *Patrisia eocenica* (7.1-58 E), *Tricolpites bibaculatus* (7.1-37 Pa; Flacourtiaceae?, see also Other Angiosperms), *Zuelania* (6.1-3 Q).

Fouquieriaceae: *Fouquieria* (4.1-25 M), *F. columnaris* (4.1-28 Q), *F. splendens* (4.1-28 Q).

Garryaceae (4.1-33 Q).

Gentianaceae (6.1-16 Q; 7.6-17 Q): *Gentiana* (7.6-2, 12, 20, 21, 23 Q), *G.* cf. *crinita* (6.1-11 Q), *Lisianthius* (6.1-2 E, 13 Pl), *Macrocarpaea* (7.6-30 Q).

Geraniaceae (4.1-33 Q; 7.6-7, 13 Q): *Geranium* (6.1-11 Q; 7.6-12, 20, 21, 23 Q).

Gesneriaceae (4.1-18 O/O–M): *Mitraria* (7.2-16 M).

Goodeniaceae: *Poluspissusites* (7.1-51 O; 7.2-10 M; see also Other Angiosperms).

Goupiaceae: *Goupioxylon stutzeri* (7.2-35, 37, M, O–M).

Gramineae (see also Maydeae, Poaceae; 4.1-18 O/O–M, 22, 23 M, 26 Pl, 30–39/40 Q; 5.1-23, 24 Q; 6.1-1–3 Q, 6 Q, 7 M, 8–20 Q, 9–11 M, 12, 15 Pl/Pl–Q, 21–23 Q; 7.1-96 E; 7.2-23, 25, 27 Pl; 7.6-2–9, 12–18, 20–25, 28–33 Q; Gramineae–Cyperaceae 6.1-15 Q): *Anatherostipa venusta* (7.6-11 Q), *Aristida adscensionis* (4.1-28 Q; 7.6-11 Q), *Bambusium stubeli* (7.2-28a, 32 M, 36 Pl), *Bouteloua aristidoides* (4.1-28 Q), *B. barbata* (4.1-28 Q), *B. simplex* (7.6-11 Q), *Bromus catharticus* (7.6-11 Q), *Chusquea* (6.1-20a Q), *Erioneuron pulchellum* (4.1-28 Q), *Euchlaena* (6.1-3 Q), *Festuca* (7.2-23, 25 Pl), *Graminidites* (4.1-11 E, O/O–M; 7.1-49, 51, 52 O; 7.2-8, 10, 13 M), *G. gramineoides* (5.1-5, 7 E), *Hilaria rigida* (4.1-28 Q), *Monoporites annulatus* (7.1-66 E–O, 100 K; 7.2-43, 50 M), *M. annuloides* (7.1-86 E), *Monoporopollenites* (7.2-45 M), *M. annulatus* (7.1-85 Pa–E), *Muhlenbergia microsperma* (4.1-28 Q), *Munroa* cf. *andina* (7.6-11 Q), *M. decumbens* (7.6-11 Q), *Nassella arcuata* (7.6-11 Q), *N. nardoides* (7.6-11 Q), *N. pubiflora* (7.6-11 Q), *P. pungens* (7.6-11 Q), *Phragmites* (7.2-23, 25 Pl), *Poacites* (5.1-15 M; 7.1-38 E; 7.2-19b, 21 M, 23, 25 Pl), *P. chloriformis* (7.1-41

E), *P. magnus* (7.2-30, 31 M), *Rhizoma graminis* (7.2-32 M, 36 Pl), *Stipa chrysophylla* (7.6-11 Q), *S. speciosa* (4.1-28 Q), *Vulpia* (4.1-28 Q), *Zea–Z. mays* (4.1-31, 33, 34, 36, 37, 39/40 Q; 5.1-24 Q; 6.1-1–3 Q, 6 Q, 8–13 Q, 18 Q, 21 Q, 22 Q; 7.6-15, 32 Q).

Griseliniaceae: *Griselinia* (7.6-12 Q), *G.* cf. *ruscifolia* (7.6-32 Q).

Grossulariaceae (see also Saxifragaceae): *Ribes* (4.1-27, 37 Q; 7.6-2, 7, 12 Q), R. *magellanicum* (7.6-3 Q).

Gunneraceae: *Gunnera* (6.1-16 Q; 7.2-39 Pl; 7.6-2, 3, 7, 9, 12, 20 Q; for pollen morphology see Wanntorp et al., 2004a), *Tricolpites* cf. *reticulatus[a]* (7.1-33, 37 Pa, 45 E, 50 ["probably *Gunnera*"], 51 O; 7.2-13 M; see also Other Angiosperms; oldest reported is *T. reticulatus* from the upper Cenomanian to Santonian [~97, 87 Ma] of Deva, Romania, and India; oldest accepted/confirmed is Turonian [~90 Ma] of Peru fide Wanntorp et al. [2004b]).

Guttiferae: *Calophyllites mesaensis* (7.2-36 Pl), *Calophyllum* (5.1-22 Q), *C. calabaformis* (5.1-17 M; 7.2-42, 44 M), *Clusia* (6.1-16 Q; 7.6-20 Q), *C. criuva* (7.6-30 Q), *C. fossilia* (7.6-30 Q), *C. vera* (7.2-44 M), Clusiaceae (7.6-13 Q), Clusiaceae–*Calophyllum* (7.6-30 Q), *Guttiferoxylon compactum* (7.1-78c O–M; 7.2-35 O–M), *G. platonioides* (7.2-35 O–M), *Hypericum* (6.1-16 Q; 7.6-8, 20 Q), *Kielmeyera* (7.6-31 Q), *K. tertiaria* (7.2-46 Pl), *Pachydermites diederexi* (4.1-22 M [*Symphonia*]; 7.2-43 M), *Rheedia* (7.2-34 M, 39 Pl), R. *miocenica* (7.2-33, 44 M), R. *pliocenica* (7.2-46 Pl), R. cf. *preacuminata* (7.1-15 E; 7.2-42 M), R. *silvargillacea* (5.1-17 M), *Symphonia* (4.1-26 Pl; 6.1-14 Pl, 18 Q; 7.6-16, 30 Q), *Vismia* (7.6-20 Q).

Haloragaceae (7.6-7 Q): *Haloragacidites amolosus* (7.2-13 M, *Haloragis*), *H. myriophylloides* (7.2-13 M, *Myriophyllum*), *Myriophyllum* (4.1-33 Q; 6.1-11 Q; 7.6-2, 6–8, 12, 13, 15, 17, 20, 33 Q), *Myriophyllumpollenites* (7.1-31, 32, 37 Pa), *Obispocaulis myriophylloides–Tarahumara sophiae* (4.1-7 K), *Tricolpites reticulata* (7.1-19 K, 29 Pa).

Hamamelidaceae: cf. *Hamamelis* (6.1-15 Pl/Pl–Q), *Liquidambar* (4.1-18 O/O–M, 26 Pl, 32, 33, 38, 39/40 Q; 5.1-10 [?] O; 6.1-3 Q, 5 Q, 6 Q, 11 Q, 13 Q, 14 Q), *L. incerta* (4.1-24 M), *L.* [?] *integrifolium* (7.1-8 K), *Liquidambarpollenites* cf. *brandonensis* (7.1-34, 35, 37 Pa), [Hamamelidaceae?, *Liquidambar* affinities?], *Tricolpites vulgaris* (7.1-34, 35 Pa).

Heliconiaceae (see also Cannaceae, Musaceae): *Heliconia* (5.1-17 M; 6.1-5 Pl, 20a Q), *H.* (or *Canna*, Cannaceae; 7.1-88 E), *H. bahiana* (7.2-47 Pl), *H. elegans* (7.2-40, 44 M), *Heliconiophyllum elegans* (7.2-36 Pl), *H. falanense* (7.2-36 Pl).

Hernandiaceae: *Gyrocarpus miocenica* (7.2-41 M), *Hernandia* (7.2-42 M), *H. tongi* (7.2-33 M), *Sparattanthelium pliocenicum* (7.2-30, 34 M).

Hippocastanaceae: *Aesculus* (4.1-25 M).

Hippocrateaceae: *Salacia floribundafolia* (7.1-15, 41 E).

Hippuridaceae: cf. *Hippuris* (6.1-15 Pl/Pl–Q).

Humiriaceae: *Humiria* (7.6-30 Q), *Humiriastrum* (7.2-39 Pl), *Psilatricolporites devriesi* (7.2-43, 50 M), *Sacoglottis* (7.2-39 Pl), *S. cipaconensis* (7.1-69, 70, 77 E), *S. costata* (Reid, 1933), *S. tertiaria* (7.2-39 Pl), *Vantanea* (7.2-39 Pl), *V. columbiana* (7.1-75 E), *V. compressiformis* (7.1-70 E), *V. sheppardi* (7.1-72 E).

Hydrangeaceae (see also Saxifragaceae): *Fendlera* (4.1-25 M), *Hydrangea* (6.1-18 Q), *H.* (?) *incerta* (7.1-8 K, 15 O), *H. serratifolia* (7.6-12 Q).

Hydrophyllaceae: *Phacelia* (4.1-28 Q; 7.6-6, 8, 11 Q).

Icacinaceae: *Citronella* (7.1-57 E), *Emmotum* (7.6-31 Q), *Villaresia congonhifolia* (7.1-41 E).

Iridaceae (7.6-7, 13, 32 Q): *Orthrosanthus* (7.6-20 Q), *Sisyrinchium* (7.6-20 Q).

Juglandaceae: *Alfaroa–Engelhardia* (6.1-2 E), *Alfaroa–Oreomunnea* (4.1-21 O/O–M, 26 Pl, 32, 38, 39/40 Q; 5.1-20 M; 6.1-8–11 M/M–Pl, 12 Pl, 15 Q), *Carya* (4.1-18 O/O–M, 23 M, 32, 33, 37 Q; 6.1-15 Pl/Pl–Q; 7.1-63 O, *Carya* type [?]), *Engelhardia* (4.1-20 O/O–M, 23 M; 5.1-10 O, now *Alfaroa–Oreomunnea*), *Engelhardtiopollenites* (7.2-45 M), *Juglans* (4.1-18 O/O–M, 25 M, 26 Pl, 31, 32, 34, 36, 38 Q, 42, Tertiary undifferentiated; 6.1-11 M/M–Pl, 11 Q, 15 Pl/Pl–Q; 7.6-7, 20, 21, 23, 25 Q), *J.* [?] *licciardoensis* (7.1-15 E), *J. linki* (7.2-29 M), *Momipites* (~*Alfaroa–Engelhardia–Oreomunnea*; 4.1-10 E), *M. anellus* (4.1-11 O/O–M), *M. corylipites* (4.1-11 E, O/O–M), *M. coryloides* (4.1-18 O/O–M), *M. microcoryphaceous* (4.1-18 O/O–M), *M. microfoveolatus* (4.1-11 O/O–M), *M. tenuipolus* (4.1-8 K), *M. triorbicularis* (4.1-18 O/O–M), *M. triradiatus* (4.1-18 O/O–M), *Paraoreomunnea* (4.1-9 E), *Platycarya swasticoida* (4.1-10 E), *Pterocarya* (4.1-18 O/O–M; 6.1-15 Pl/Pl–Q).

Juncaceae (7.6-7, 20 Q): *Juncus* (7.2-39 Pl).

Juncaginaceae (7.6-7 Q).

Krameriaceae: *Krameria grayi* (4.1-28 Q), *K. lappacea* (7.6-11 Q).

Labiatae (4.1-18 O/O–M, 32, 37 Q; 5.1-23 Q; 7.6-6, 7, 13, 32 Q): *Hyptis* (7.6-25, 30–32 Q), *H. emoryi* (4.1-28 Q), *Salvia killipiana* type (7.6-20 Q), *S. polystachia* (4.1-27 Q), *S.* type (7.6-8 Q), *Satureja* (4.1-37 Q), *S. nubigena* type (7.6-20 Q).

Lactoridaceae: *Lactoris* (7.2-8 M).

Lamiaceae (see Labiateae).

Lardizabalaceae: *Boquila* (7.2-16 M).

Lauraceae (see also possibly some *Laurophyllum* cited under Other Angiosperms): *Acrodiclidium chartaceum* (7.2-32 M, 36 Pl), *A. oligocaenicum* (7.1-15, 41, 58 E; 7.2-19a M), *A. pseudocanelo* (5.1-8 O), *A. pseudosalicifolium* (5.1-8 O), *Aiouea* (7.1-57 E), *Ampelodaphne grandifolia* (7.1-41, 58 E; 7.2-19a M), *Aniba collazoensis* (5.1-8 O), *Camphoromoea speciosa* (7.1-15, 57, 58 E; 7.2-19a, 30, 31 M), *Cinnamomum* (7.1-15 E), *C. heeri* (7.1-8 K), *C. incertum* (7.2-46 Pl), *Cryptocarya* (7.1-57 E), *Cryptocaryoides maria-santisimensis* (7.1-28 Pa), *Goeppertia* (Marantaceae; 7.1-15 E), *G. engelhardti* (7.1-58 E), *G. ovalifolia* (7.1-41, 58 E; 7.2-19a M), *G. spectabilis* (7.1-58 E; 7.2-19a M), *G. subherbacea* (7.2-32 M, 36 Pl), *G. tertiaria* (4.1-24 M; 6.1-5 Pl), *Hufelandia portoricensis*

(5.1-8 O), *Laurinium beilschmiedioides* (7.1-54 K), *Laurophyllum* (7.2-16 M), *L. actinodaphnoides* (7.1-15, 58 E; 7.2-19a M), *L.* (*Nectandra*) *chubutensis* (7.1-28 Pa), *L. kurtzi* (7.2-5 M), *L.* (*Oreodaphne*) *piatnitzkyi* (7.1-28 Pa), *L. rigidum* (7.2-32 M), *L.* sp. 1, 2 (7.1-15 E), *Mespilodaphne acrensis* (7.2-34 M), *M. colombiana* (7.2-33 M), *M. culebrensis* (6.1-6 M/M–Pl), *M. hispaniolana* (5.1-16 M), *M. lojana* (7.2-30 M), *M. longifolia* (7.1-15, 58 E; 7.2-19a M), *M. palomaresensis* (4.1-24 M), *M. tumbezensis* (7.2-28a M), *Misanteca dubiosa* (5.1-8 O), *Nectandra* cf. *antillanafolia* (7.1-88 E), *N. areolata* (4.1-24 M; 6.1-5 Pl; 7.2-32 M, 36 Pl), *N. chilana* (7.1-15, 58 E), *N. curvatifolia* (7.2-32 M, 36 Pl, 42, 44 M), *N. kugleri* (7.2-44 M), *N. patagonica* (7.1-41 E; 7.2-19b M), *N. prolifica* (7.1-15, 41, 57 E), *N. reissi* (7.2-30, 32 M, 36 Pl), *N. saltensis* (7.2-6 M), *N. silvarenaria* (7.2-44 M), *N. tehuantepecensis* (4.1-24 M), *N. woodringi* (6.1-5 Pl), *Nectandrophyllum* (7.2-19a M), *Nothophoebe neogaea* (7.1-15, 41 E), *N. ovatifolia* (7.1-15, 41 E), *Ocotea* (6.1-15 Pl/Pl–Q; 7.2-16 M; 7.6-32 Q), *O.* cf. *rubra* (7.2-36 Pl), *Oreodaphne mississippiensis* (5.1-8 O), *O. piatnitzkyi* (7.1-15 E), *O. preacutifolia* (7.1-41 E), *Persea* (4.1-1 K, 25 M; 6.1-15 Pl/Pl–Q; 7.2-14, 16 M), *P. americana* (7.6-26 Q), *P. coriacea* (7.2-30, 32, 33 M, 36 Pl), *P. elliptica* (7.2-32 M, 36 Pl), *P. elongata* (7.2-32 M, 36 Pl), *P. macrophylloides* (7.1-58 E; 7.2-19a, 28a, 32 M, 36 Pl, 42, 44 M), *P. microphylla* (7.1-15, 58 E; 7.2-19a M), *P. preamericana* (7.2-42, 44 M), *Phoebe* (7.2-16 M), *P. elliptica* (7.1-41, 57, 58 E; 7.2-19a M), *P. lanceolata* (7.1-15, 41, 58 E; 7.2-19a M), *Sassafras* [?] *acutilobum* (7.1-8 K), *S. cretaceum* (7.1-8 K), *S. mudgei* (7.1-8 K), *S. subintegrifolium* (7.1-8 K), *Ulminium atlanticum* (7.1-39 E).

Lecythidiaceae: *Cercophora* type (7.6-8 Q), *Couroupita* (6.1-18 Q), *C. ovata* (7.2-46 Pl), *C. santanderensis* (7.2-33 M), *C. tertiaria* (7.2-30 M), *Gustavia* (4.1-26 Pl), *Lecythidoanthus kugleri* (7.2-44 M), *Lecythidophyllum couratarioides* (4.1-24 M), *Lecythidospermum bolivarensis* (7.1-78b O–M), *Lecythis nerifolia* (7.1-58 E).

Leeaceae (see also Vitaceae): *Leea* (4.1-9 E).

Leguminosae (4.1-18 O/O–M, 37 Q; 7.6-4, 8, 16, 25, 30–32 Q): *Acacia* (4.1-18, 19 O/O–M, 25 M, 26 Pl; 5.1-10 O; 6.1-3 Q, 7, 10 M, 12 Q, 15 Pl/Pl–Q, 17 Q; 7.1-66 E–O; 7.6-7, 25, 30 Q), *A. dimidiato-cordata* (7.2-21 M, 23, 25 Pl), *A. eocaribbeanensis* (5.1-18 M), *A. greggii* (4.1-28 Q), *A. tenuifolia* (7.2-21 M, 23, 25 Pl), *A. uninervifolia* (7.2-21 M, 23–25 Pl), *Acaciapollenites myriosporites* (7.2-9, 13 M, see also Other Angiosperms), *Acacioxylon* (4.1-41 Tertiary undifferentiated; see also Other Angiosperms), *A. o'donellii* (7.2-7 Pl), *A. pseudocavenium* (7.1-54 K, *Acacia*), *Adesmia* (7.6-2, 8, 11 Q), *A. atacamensis* (7.6-11 Q), *Aeschynomene* (7.6-31 Q), *A. bolivianum* (7.2-23, 25 Pl), *Aetanthus* (5.1-10 O), *Amicia antiqua* (7.2-22 M, 23, 24, 25 Pl), *Anarthrophyllum* (7.6-4, 8 Q), *Andira* type (7.6-31 Q), *Astragalus nuttalianus* (4.1-28 Q), *Bauhinia* (6.1-15 Pl/Pl–Q), *B. ecuadorensis* (7.2-30 M), *B. emarginata* (6.1-18 Q), *B. potosiana* (7.2-23, 25 Pl), *Brownea* (7.2-39 Pl), *Caesalpinia* (4.1-25 M; 5.1-24 Q; 6.1-12 Pl), *C. echinataformis* (7.2-47 Pl), *C. gmehlingi* (7.2-21 M, 23, 25 Pl), *C. potosianus* (7.2-23, 25 Pl), *C. prebahamensis* (5.1-17 M), *C. sessilifolioides* (7.2-23, 25 Pl), *C. subdimidiata* (7.2-30, 31 M), *Caesalpinites incertus* (5.1-17 M), *Calliandra* (6.1-17 Q, 18 Q; 7.2-11 M; 7.6-31, 32 Q), *C. obliqua* (7.2-21 M, 23–25 Pl), *C. ovatifolia* (7.2-21 M, 23, 25 Pl), *Canavalia* (6.1-18 Q), *C. miocenica* (7.2-44 M), *Cassia* (4.1-25 M; 7.6-20, 30–32 Q), *C. aguaytiensis* (7.2-28b, 34 M), *C. argentinensis* (7.1-41 E; 7.2-14 M), *C. bassleri* (7.2-28b, 30 M), *C. bigidulifolia* (7.2-23 Pl), *C. chrysocarp[i]oides* (7.2-20–22 M, 23, 25 Pl), *C. cristoides* (7.2-20, 22 M, 23, 25 Pl), *C. culebrensis* (6.1-6 M/M–Pl), *C. cultrifoliaformis* (7.2-23, 25 Pl), *C. dimidiato[-]linearis* (7.2-30, 31 M), *C.* (?) *dubiosa* (5.1-8 O), *C. evidens* (5.1-8 O), *C. fonsecana* (7.2-47 Pl), *C. franckei* (7.2-23, 25 Pl), *C. gardneri* (7.1-58 E), *C. imitativa* (5.1-8 O), *C. imparilis* (5.1-8 O), *C. kugleri* (7.2-44 M), *C. leptocarpoides* (7.2-42, 44 M), *C. ligustrinaformis* (7.2-23–25 Pl), *C. ligustrinoides* (7.2-20–22 M), *C. linearifolia* (7.2-30, 31 M), *C. longifolia* (7.1-15 E, 41, 58 E; 7.2-30, 31, 44 M), *C. marahiana* (7.2-46 Pl), *C. membranacea* (7.2-21 M, 23, 25 Pl), *C. obscura* (7.2-21 M, 23, 25 Pl), *C. obtusatafolia* (7.2-47 Pl), *C. ordinaria* (5.1-8 O), *C. oxleyi* (7.1-41, 58 E), *C. patagonica* (7.1-41 E), *C. puyearensis* (5.1-8 O), *C. rigidulifolia* (7.2-21 M, 23, 25 Pl), *C. singewaldi* (7.2-23–25 Pl), *C. sipariensis* (7.2-44 M), *C. visibilis* (5.1-8 O), *C. wendtii* (7.2-22 M, 23, 25 Pl), *C. yumuriensis* (5.1-17 M), *C. zuliana* (7.2-34, 44 M), *Celtis* (4.1-25 M), *Cercidium floribundum* (4.1-28 Q), *C. floridum* (4.1-28 Q), *C. microphyllum* (4.1-28 Q), *Copaifera* (6.1-15 Pl/Pl–Q, 18 Q; 7.6-30, 31 Q), *C. corocoriana* (7.2-23–25 Pl), *C. potosiana* (7.2-23, 25 Pl), *C. reticulata* (7.1-58 E; 7.2-19a M), *Copaiva* [*Copaifera*] *oligocenica* (5.1-8 O), *Crassiectoapertites columbianus* (7.2-50 M), *Crotalaria* (7.6-8, 30 Q), *Crudia* (4.1-21 O/O–M; 6.1-2 E, 8–10 M), *Crudioxylon pinalense* (7.2-38 Pl), *C.* sp. (7.2-38 Pl), *Cynometra rabellii* (5.1-8 O), *Dalbergia* (4.1-39/40 Q), *D. antiqua* (7.2-21 M, 23–25 Pl), *D. chartacea* (7.2-21 M, 23, 25 Pl), *D. ettinghauseni* (7.2-46 Pl), *D. hesperia* (5.1-17 M), *D. patagonica* (7.1-41 E), *D. potosiana* (7.2-23, 25 Pl), *Dalea* (4.1-25 M; 7.6-20 Q), *D. mollis* (4.1-28 Q), *D. mollissima* (4.1-28 Q), *Desmodium ellipticum* (7.2-21 M, 23, 25 Pl), *D. obliqui[u]m* (7.1-58 E; 7.2-19a M), *Dioclea* (7.6-30 Q), *D.* (?) *mexicana* (4.1-24 M), *Drepanocarpus franckei* (7.2-21 M, 23–25 Pl), *D.* type (6.1-18 Q), cf. *Enterolobium* (6.1-15 Pl/Pl–Q), *E. grandifolium* (7.2-21 M, 23–25 Pl), *E. parvifolium* (7.2-21 M, 23, 25 Pl), *Eperua* (4.1-23 M), cf. *Eriosema* (7.6-20 Q), *Erythrina* (6.1-10 M, 17 Q, 18 Q), *E. glauca* (6.1-18 Q), *Eysenhardtia* (4.1-25 M), *Geoffroea* (7.6-7 Q), *G. pfaffia* (7.6-32 Q), cf. *Haematoxylon* (6.1-3 Q, 15 Pl/Pl–Q), *Hedysarum bolivianum* (7.2-21 M), *Hoffmanseggia* (7.6-11 Q), *Hymenaea* (amber spectrum; 4.1-11 O; see also Miocene Dominican amber; 7.6-30 Q), *Inga* (6.1-15 Pl/Pl–Q; 7.6-30 Q), *I. curta* (5.1-8 O), *I. engelhardti* (7.2-30 M), *I. eolaurina* (7.1-88 E), *I. kugleri* (7.2-44 M), *I. latifolia* (7.2-31 M), *I. leonii* (5.1-17 M), *I. lojana* (7.2-30, 34 M), *I. miocenica* (4.1-24 M; 5.1-17 M), *I. myrianthafolia* (7.2-46 Pl), *I. ochseniusi* (7.2-21 M, 23, 25 Pl), *I. oligocaenica* (6.1-6 M/M–Pl), *I. ovalifolia* (7.2-31 M), *I. patagonica* (7.1-41 E), *I. pseudinsignis* (5.1-8 O), *I. pseudonobilis* (5.1-8 O), *I. pseudospuria* (5.1-8 Q), *I. reissi* (7.2-32, 34 M, 36 Pl), *I. sanchezensis* (5.1-15 M), *I. sheroliensis* (6.1-5 Pl), *I.* sp. (5.1-8 O, 15 M), *Lathyrus* (7.6-20 Q), *Leguminosites* (7.1-57 E; see also Incertae sedis), *L. acaciaeformis* (7.2-31 M), *L. bahiensis* (7.2-46 Pl), *L. belensis* (7.1-70 E), *L. braziliensis* (7.2-46 Pl), *L. canavaliformis* (7.2-44 M), *L. caseareana* (7.2-34 M), *L. cassioides* (7.2-30, 31 M), *L. copaiferaeoides* (7.1-58 E; 7.2-19a M), *L. cuquensis* (7.2-41 M), *L. engelhardti* (7.2-30 M), *L. entadaformis* (7.2-40 M), *L. erythrinoides*

(7.1-58 E; 7.2-19a M), *L. globularis* (7.2-23, 25 Pl), *L. grandis* (7.2-30, 31 M), *L. hymenaeoides* (7.2-46 Pl), *L. machaerioides* (7.2-31 M, 46 Pl), *L. mexicanus* (4.1-24 M), *L. mucunoides* (7.1-69, 70 E), *L. oaxacensis* (4.1-24 M), *L. patagonicus* (7.2-19b M), *L. silvensis* (7.2-44 M), *L. trinitensis* (7.2-44 M), *L. venezuelensis* (7.2-40 M), *Leguminoxylon grossei* (7.1-78c O–M; 7.2-35 O–M), *Leptolobium eonitens* (7.2-46 Pl), *L. prenitens* (7.1-41 E), *Leucaena multicapitula* (6.1-18 Q), *Lonchocarpus engelhardti* (7.2-30 M), *L. obtusifolius* (7.2-21 M, 23, 25 Pl, 31 M), *L. praelatifolius* (5.1-8 O), *Lotus strigosus* (4.1-28 Q), *Lupinus* (7.6-20 Q), *L. arizonicus* (4.1-28 Q), *L. concinnus* (4.1-28 Q), *Lysiloma* (4.1-25 M), *Machaerium* (7.2-39 Pl; 7.6-30 Q), *M. eriocarpoides* (7.2-21 M, 23–25 Pl), *M. milleri* (7.2-23, 25 Pl), *Macrolobium* (7.6-25 Q), *M. tenuifolium* (7.2-30, 31 M), *Margocolporites vanwijhei* (7.1-66 E–O, 85 Pa–E; 7.2-10, 43, 50 M; cf. *Caesalpinia*; see also Other Angiosperms), *Mimosa* (4.1-26 Pl, 39/40 Q; 7.6-30–33 Q), *M. arcuatifolia* (7.2-21 M, 23–25 Pl), *M. montanoides* (7.2-21 M, 23, 25 Pl), *M.* cf. *scabrella* (7.6-32 Q), *Mimosites* [7.2-21 M; see also Incertae sedis] *engelhardti* (7.2-23–25 Pl), *M. linearis* (7.2-25 Pl), *M. suteri* (7.2-41 M), *Mucuna* (6.1-18 Q), *Myroxylon* cf. *balsamum* (6.1-15 Pl–Q), *Olneya tesota* (4.1-28 Q), *Peltophorum membranaceum* (7.2-21 M, 23–25 Pl), *Phaseolus* (7.6-20 Q), *Piptadenia* (7.6-32 Q), *Piscidia* (4.1-25 M, 39/40 Q; 6.1-10 Q), *Pithecellobium* (4.1-25 M; 6.1-15 Pl/Pl–Q), *P. brittonianum* (7.2-23, 25 Pl), *P. ecuadorensis* (7.2-30 M), *P.* (?) *imperfectum* (5.1-8 O), *P. pre[-]saman* (7.2-28b, 30 M; 7.2-34 M, *Pithecolobium*), *P. pseudotrapezifolium* (5.1-8 O), *P. samanensis* (5.1-15 M), *P. tenuifolium* (7.2-32 M, 36 Pl; 7.2-44 M, *Pithecolobium*), *P. tertiarium* (7.2-21 M, 23, 25 Pl), *P. unguis* (7.6-26 Q), *P. vexativum* (5.1-8 O), *P. yumuriensis* (5.1-17 M), *Plati[y]podium potosianum* (7.2-21 M, 23, 25 Pl), *Polyadopollenites* (7.2-9, 10, 50 M, cf. *Acacia*, *Inga*; see also Other Angiosperms), *P. mariae* (7.2-43, 50 M, *Acacia*), *Prosopis* (4.1-30 Q; 7.6-4, 7 Q), *P. velutina* (4.1-28 Q), *Psilatriporites desilvae* (7.2-50 M, Caesalpinioideae), cf. *Pterocarpus* (6.1-15 Pl/Pl–Q), *P. officinalis* type (6.1-18 Q), *P.–Sclerolobium* (7.6-30 Q), *Pterogyne oblongifolium[-a]* (7.2-30, 31 M), *Retitricolporites poriconspectus* (7.2-50 M), *Robinia* (4.1-25 M), *Schizolobium inaequilaterum* (7.1-98 E), cf. *Senna* (7.1-57 E; 7.2-16 M), *Sophora cookei* (5.1-15 M), *S. maranoides* (5.1-17 M), *S. matanzana* (5.1-17 M), *S. salvadorana* (7.2-40 M), *S.* (?) *suspecta* (5.1-8 O), *S. yumuriensis* (5.1-17 M), *Stenolobium rhomboidalis* (7.1-15 E; 7.2-30, 31 M), *Striatricolpites catatumbus* (5.1-7 E; 7.1-85 Pa–E, 86, 87 E; 7.2-43, 50 M; cf. *Crudia* type; see also Other Angiosperms), *Stryphnodendron* (7.6-30, 31 Q), *Swartzia panamensis* type (6.1-18 Q), *Sweetia tertiaria* (7.2-20, 21 M, 23, 25 Pl), *Swer[e?]tia tertiaria* (7.2-22 M), *Taenioxylon multiradiatum* (6.1-6 M/M–Pl), *Tapirira durhamii* (4.1-19 O/O–M), *Tipuana ecuadoriana* (7.2-30 M), *Trifolium* type (7.6-8 Q), *Triptolemea tertiaria* (7.2-34 M, 47 Pl), *Vicia* (7.6-20 Q).

Leguminosae–Caesalpinioideae–Caesalpiniaceae (4.1-18 O/O–M).

Leguminosae–Mimosoideae–Mimosaceae (4.1-37 Q; 7.6-20, 29, 30, 32 Q).

Leguminosae–Papilionoideae–Papilionaceae (4.1-33, 37 Q; 7.6-6, 7, 20 Q).

Lemnaceae: *Lemna* (4.1-32 Q).

Lentibulariaceae (7.6-30 Q): *Utricularia* (4.1-26 Pl, 33 Q; 5.1-23 Q; 6.1-9, 10 M; 7.6-20, 32 Q).

Liliaceae (4.1-18 O/O–M, 30): *Allium* type (6.1-11 Q), *Astelia pumila* (7.6-3, 12 Q), *Liliacidites* (4.1-23 M; 7.1-52 O–M, 80 K; 7.2-45 M; see Bromeliaceae, Palmae, Other Angiosperms), *L. kaitangataensis* (7.1-56 Pa), *L. variegatus* (4.1-11 O/O–M; 7.1-51 O; 7.1-55 K), *Smilacipites saltensis* (7.1-34, 35 Pa, 50 O; *Smilax*).

Limnochariaceae: *Limnocharis* (6.1-19 Q, 20 Q).

Loasaceae: *Mentzelia involucrata* (4.1-28 Q).

Loganiaceae (see also Strychnaceae): *Antonia* (7.6-31 Q), *Buddlei(j)a cordata* (4.1-27 Q), *Desfontainia* (7.2-16 M), *Rhiopites minusculus* (7.1-37 Pa; see also Other Angiosperms), *Strychnos mirhojana* (7.2-19b M), *S. patagonica* (7.1-41 E).

Loranthaceae (6.1-10 M; 7.6-20, 30, 32 Q): *Antidaphne* (6.1-16 Q), *A.* (?) *lotensis* (7.1-58 E), *Arceuthobium* (4.1-32–34, 36 Q), *Gaiadendron* (6.1-16 Q); *G. punctatum* (7.6-20 Q), *Gothanipollis bassensis* (7.1-45 E), *Lepidoceras kingii* (7.6-12 Q), *Oryctanthus* (5.1-20 M), *O. cordifolius* (6.1-18 Q), *Phoradendron californicum* (4.1-28 Q), *P. fossile* (7.2-30, 31 M), cf. *Psittacanthus* (6.1-14 Pl), *P. crassifolius* (7.1-58 E; 7.2-19a M), *Srivastapollenites exoticus* (7.1-19 K, 36 Pa, Loranthaceae?), *Struthanthus* (4.1-26 Pl; 6.1-14 Pl; 7.6-32 Q), *Syndemicolpites petriellai* (7.1-29 Pa), *Tristerix* (7.6-12, 20, 32 Q), *T. longebracteatus* type (7.6-20 Q).

Lythraceae (6.1-11 Q; 7.2-39 Pl): *Cuphea* (4.1-26 Pl, 33 Q; 5.1-23 Q; 7.6-20, 30, 31 Q), *C. antiqua* (7.2-22 M, 23, 25 Pl), *C.* cf. *ingrata* (7.6-32 Q), *C.* cf. *urbaniana* (7.6-32 Q), *Lafoensia* (6.1-18 Q; 7.6-31 Q), *Verrutricolporites* (7.2-45 M, Lythraceae?), *V. rotundiporus* (7.2-43 M, cf. *Crenea*).

Magnoliaceae: *Drimys* aff. *patagonica* (7.1-15 E), *Magnolia* (6.1-20a Q), *Peninsulapollis gillii* (7.1-20 K; Magnoliaceae?).

Malpighiaceae (4.1-18 O/O–M; 5.1-20 M, 23 Q; 6.1-2, 3, 5 Q, 7, 9, 10 M, 11 Q, 13 Q, 14 Q, 17 Q, 18 Q; 7.1-94 O–M, 96 Pa; 7.2-16 M; 7.6-20 Q): cf. *Acridocarpus* (6.1-15 Pl/Pl–Q), *Banisteria* (6.1-15 Pl/Pl–Q), *B. aceroides* (7.2-30, 31 M), *B. bassleri* (7.2-28b M), *B. incerta* (7.2-28a M), *B. oblongifolia* (7.2-47 Pl), *B. patagonica* (7.1-41 E), *B. praenuntia* (6.1-6 M/M–Pl), cf. *Banisteriopsis* (6.1-13 Pl), *Bunchosia* (5.1-23 Q), *Byrsonima* (4.1-39/40 Q; 6.1-1 Q, 2 Q, 9 Q, 11 Q, 18–20 Q; 7.6-25, 29, 30 Q), *B. bullata* (7.1-98 E), *B. crassifolia* (6.1-17 Q), *Hiraea* (4.1-26 Pl; 6.1-15 Pl/Pl–Q), *H. cyclosperma* (7.2-30, 31 M), *H. oligocaenica* (6.1-6 M), *Malpighia* (4.1-26 Pl), *Mascagnia sepiumoides* (7.1-41 E), cf. *Mezia* (?) type (4.1-26 Pl), *Perisyncolporites pokornyi* (7.1-85 Pa–E; 7.2-43, 50 M; see also Other Angiosperms), *Tetrapterys precrebrifolia* (7.1-15, 41 E).

Malvaceae (4.1-33, 37, 39/40 Q; 5.1-23 Q; 6.1-9 M, 11 Q, 18 Q; 7.1-61 E [Malvaceae type, age uncertain], 94 O–M; 7.6-4, 6, 13, 20, 30, 32 Q): *Abutilon* (5.1-10 O), *Acaulimalva purpurea* (7.6-20 Q), *Baumannipollis chubutensis* (7.2-13 M), *B. variaperturatus* (7.1-51, 52 O; 7.2-8, 10 M; see also Other Angiosperms), *Cristaria* (7.6-11 Q), *Echiperiporites akanthos* (7.1-66 E–O; see also Other Angiosperms), *E. estelae* (7.1-66 E–O, larger forms

cf. *Hibiscus*; 7.1-85 Pa, cf. *Hibiscus*, *Thespesia*; 7.2-43 M; see also Other Angiosperms), *Gossypium* (6.1-12 Q), *Hampea–Hibiscus* (4.1-26 Pl; 6.1-7, 10 M), *Hibiscus* (7.6-30 Q), *Horsfordia newberryi* (4.1-28 Q), *Lakiapollis* aff. *ovatus* (7.1-85 Pa–E), *Malvacarpus guinazui* (7.1-41 M), *M. octoloculus* (7.1-70 E), *M. tertiarius* (7.2-19b M), *Malvacipollis argentina* (7.1-47 E), *M. diversus* (7.1-56 Pa, *Hoheria*), *Malvacipolloides comodoroensis* (7.2-8, 10, 13; see also Other Angiosperms), *Malvastrum* (7.6-23 Q), *Malvocarpon clarum* (5.1-8 O), *Sida* (7.6-25 Q), *Sphaeralcea* (4.1-28 Q), *Tarasa operculata* (7.6-11 Q), *T.* type (7.6-8 Q).

Marantaceae: *Goeppertia* (see Lauraceae).

Marcgraviaceae: *Marcgravia* (5.1-10 O), *Norantea* (4.1-23 M; 5.1-10 O).

Maydeae (Gramineae; 4.1-33 Q).

Melastomataceae (4.1-39/40 Q; 5.1-23, 24 Q; 6.1-1 Q, 7 Q, 10 M, 10 Q, 13 Pl, 15 Pl/Pl–Q, 16, 22 Q; 7.1-94 O–M; 7.2-39 Pl; 7.6-13, 16, 20–25, 30–32 Q): *Heterocolpites incomptus* (7.2-50 M), *H. palaeocenica* (7.1-84 Pa; see also Other Angiosperms), *H. paluster* (7.1-86 E), *H. verrucosus* (7.2-50 M), *Huberia preovalifolia* (7.2-46 Pl), Melastomataceae–Combretaceae (7.6-28, 29 Q), Melastomataceae–*Terminalia* (6.1-2 Q), *Melastomaceophyllum danielis* (7.1-78a E), *Melastomites* (7.2-30 M), *M. angustus* (4.1-24 M), *M. domingensis* (5.1-15 M), *M. miconioides* (6.1-6 M/M–Pl), *M. obovatus* (4.1-24 M), *M.* sp. (5.1-15 M), *Melastomophyllum* (7.2-16 M), *Miconia* (7.6-15, 17, 20 Q), *M. ettinghauseni* (7.2-46 Pl), *M. prealbicans* (7.2-46 Pl), *Tibouchina dolianitii* (7.2-48 Pl), *T. santosii* (7.2-48 Pl).

Meliaceae (4.1-18 O/O–M; 5.1-23, 24 Q; 6.1-2 Q, 19 Q; 7.6-20, 31 Q): *Cabralea* (7.6-31 Q), *Cedrela* (4.1-21 O/O–M, 26 Pl; 6.1-10 M, 15 Pl/Pl–Q; 7.6-20, 30 Q), *C. campbeli* (7.2-47 Pl), *C.* cf. *fissilis* (7.6-32 Q), *C. jacksoniana* (7.1-89 E), *C. mexicaniformis* (7.1-41 E), *C. miocenica* (4.1-24 M), *C. pichileufuana* (7.1-41 E), *C. preodorata* (7.2-42, 44 M), *C.* (?) *tertiaria* (7.2-44 M), *Guarea* (4.1-21 O/O–M, 26 Pl; 5.1-10 O; 6.1-10 M; 7.6-20 Q), *G. opinabilis* (5.1-8 O), cf. *Hiraea* (6.1-13 Pl), Meliaceae–Sapotaceae (6.1-18 Q), *Moschoxylun falcatum* (7.1-58 E; 7.2-19a M), *M. tenuinerve* (7.1-58 E; 7.2-19a, 32 M, 36 Pl), *Pachyexinus* (7.1-85 Pa–E), *Swietenia mahagoniformis* (5.1-17 M), *Tetracolporites spectabilis* (7.2-10 M), *Trichilia* (7.6-30–32 Q), *T. branneri* (7.2-46 Pl), *T. catignoides* (7.1-41 E), *T. evidens* (5.1-8 O), *T. hirtaformis* (5.1-17 M; 7.2-30, 42, 44 M), *T. moritziformis* (7.1-41 E), *T. pseudobakerii* (5.1-8 O), *T. pseudohirta* (5.1-8 O), *T. spatulata* (5.1-8 O).

Mendonciaceae (Acanthaceae): *Mendoncia* (6.1-18 Q), *Venezuelites globoannulatus* (7.2-43 M).

Menispermaceae (6.1-18 Q).

Menyanthaceae: cf. *Nymphoides* (4.1-33 Q), *N. grayana* (5.1-23 Q).

Mimosaceae (6.1-11 Q, 18 Q; see also Leguminosae): *Rhoipites baculatus* (7.1-37 Pa; see also Other Angiosperms).

Misodendraceae: *Misodendrum* (7.6-2, 3, 7, 12 Q).

Monimiaceae (Antherospermataceae): *Doryphora* (7.2-16 M), *Laurelia* (7.1-9 K; 7.6-12 Q), *L. amarillana* (7.1-8 K), cf. *L. guinazui* (7.1-15, 41 E), *L. insularis* (7.1-15 E), *Laurelites doroteaensis* (7.2-15 M), *Laurelioxylon intermedium* (7.1-54 K), *Peumus* (7.1-25–27 Pa; see also Other Angiosperms), *P. clarki* (7.2-19b M), *Siparuna preguayensis* (7.2-47 Pl, Siparunaceae).

Moraceae (4.1-18 O/O–M, 39/40 Q; 5.1-23 Q; see also Urticaceae): *Brosimum* (4.1-39/40 Q; 6.1-1 Q, 9–11 Q), *B. miocenicum* (7.2-44 M), *Cecropia* (7.2-39 Pl), *Chlorophora* (4.1-39/40 Q; 6.1-1 Q; 7.6-25 Q), *Clarisia* (7.6-25 Q), *Coussapoa* (7.2-33 M), *C. carrioni* (7.2-30 M), *C. prepliocenica* (7.1-15 E), *C.* (?) *quinquenervis* (7.1-58 E), *C. vaningeni* (7.2-44 M), *Coussapoites portae* (7.2-36 Pl), *C.* aff. *veracruziana* (7.2-36 Pl), *Dorstenia* (4.1-18 O/O–M), *Ficus* (5.1-22, 23 Q; 6.1-2 E, 11 Q, 15 Pl/Pl–Q), *F. americanafolia* (7.1-89 E), *F. aramaryensis* (7.2-46 Pl), *F.* cf. *betijoquensis* (7.2-33, 34, 40 M), *F.* cf. *cotinifolius* (6.1-15 Pl/Pl–Q), *F. culebrensis* (6.1-6 M/M–Pl), *F. hyphodroma* (5.1-8 O), *F. laqueata* (7.2-32 M, 36 Pl), *F. mamilliferafolia* (7.2-46 Pl), *F. patagonica* (7.1-41 E), *F. porcellanaria* (7.2-44 M), *F. schimperii* (5.1-8 O), *F. sphericus* (7.1-70 E), *F. talamancana* (4.1-24 M; 6.1-5 Pl; 7.2-33 M), *F. tressensii* (7.2-6 M), *F. vexativus* (5.1-8 O), *F. winslowiana* (7.2-28a M), *F.* sp. (5.1-8 O), Moraceae–Urticaceae (6.1-2, 3, 5, 6, 8, 11–14, 17, 19 Q; 7.6-8, 13, 14, 16, 20, 23, 28, 29, 31, 33 Q), *Pseudolmedia spuriaformis* (5.1-17 M), *Psiladiporites* (7.2-45 M), *P. minimus* (7.2-43, 50 M), *P. redundantis* (7.2-50 M), *Trophis* (4.1-39/40 Q; 6.1-10 Q).

Musaceae (see also Heliconiaceae): *Musophyllum* (5.1-8 O), *M. elegans* (7.2-32 M).

Myrantaceae (6.1-20a Q).

Myricaceae: *Myrica* (4.1-26 Pl, 33, 34, 39/40 Q; 6.1-2, 3, 11, 12 Q, 15 Pl/Pl–Q, 16–19 Q, 23 Q; 7.6-8, 13, 17, 20, 21, 23 Q), *M. annulites* (4.1-8 K), *M. banksioides* (7.2-21, 22 M, 23, 25 Pl), *M. cerifera* (5.1-23 Q), *M. engelhardtii* (7.2-22 M, 23 Pl), *M. mira* (7.1-41 E; 7.2-19b M), *M. potosina* (7.2-22 M), *M.* [?] *premira* (7.1-15 E, 28 Pa), *M. wendtii* (7.2-21, 22 M, 23 Pl), *Myricipites* (7.2-45 M), *Myricophyllum* (7.2-21 M, 23, 25 Pl), *Triatriopollenites bertelsii* (7.1-29 Pa; see also Other Angio-sperms), *T. lateflexus* (7.1-45 E; see also Other Angiosperms).

Myristicaceae: *Compsoneura* (6.1-18 Q), *Dialyanthera* (6.1-18 Q), *Myristica fossilis* (7.1-15, 41, 58 E; 7.2-19a, 30, 31 M), *Myristicophyllum panamense* (6.1-6 M/M–Pl), *Retimonocolpites absyae* (7.2-50 M, *Virola*), *Virola* (6.1-18 Q).

Myrsinaceae: *Ardisia crassifolia* (7.1-41, 58 E; 7.2-19a M), cf. *Conomorpha* (7.6-20 Q), *Geissanthus brittoni* (7.2-42 M), *Icacorea prisca* (5.1-8 O), *I.* sp. (5.1-8 O), *Myrsine* (6.1-16 Q; 7.6-14, 15, 17, 29, 33 Q), *M. braziliana* (7.2-47 Pl), *M. ciliatafolia* (7.2-46 Pl), *M. eomyricoides* (7.2-30 M), *M. pseudoferruginea* (5.1-8 O), *Rapanea* (7.1-57 E; 7.6-20, 21, 24, 25, 30–32 Q), *Stylogyne* (?) *fragmenta* (5.1-8 O), *Virola tertiaria* (7.1-70 E).

Myrtaceae (4.1-18 O/O–M; 5.1-23, 24 Q; 6.1-2 Q, 3 Q, 11 Q, 15 Pl/Pl–Q, 16 Q, 18–20 Q; 7.1-94 O–M, 96 E; 7.6-6–9, 12, 14, 16, 20, 23, 25, 28–33 Q): *Agonis* (7.2-16 M), *Amomyrtoxylon palaeolumum* (7.1-54 K, *Amomyrtus*), *Amomyrtus* (7.2-16 M),

Aulomyrcia (7.2-16 M), *Callistemon* (7.2-16 M), *Calyptranthes domingensis* (5.1-15 M), *C. gatunensis* (6.1-6 M/M–Pl), *C. marahiensis* (7.2-46 Pl), *Eucalyptus patagonicus* (7.2-2 M), *Eugenia* (5.1-10 O; 6.1-15 Pl/Pl–Q, 3 Q; 7.6-20 Q), *E. co[a]mparabilis* (5.1-8 O; 7.2-33, 42, 44 M), *E. ovalifolia* (7.2-30, 31 M), *E. ovatifolia* (5.1-17 M), *E. pseudaeruginea* (5.1-8 O), *Eugenia–Myrcia* (4.1-21 O/O–M, 26 Pl; 6.1-2 E, 7, 8, 10 M, 13 Pl), *Jambosa lanceolata* (7.2-32 M, 36 Pl), *Lecythis* (Lecythidaceae; 7.1-15 E), *L. neriifolia* (7.2-19a M), *Myrceugenellites maytenoides* (7.2-15 M), *Myrceugenelloxylon pseudoapiculatum* (7.1-54 K, *Myrceugenella*), *Myrceugenia* (7.2-16 M), *M. tertiaria* (7.1-41 E), *Myrcia* (5.1-10 O; 7.2-16 M), *M. acutifolia* (7.1-8 K; 7.2-5 M), *M. antediluviana* (7.2-30, 31 M), *M. banksioides* (7.2-20 M), *M. cajamarcana* (7.2-30 M), *M. chubutensis* (7.1-15, 41 E; 7.2-19b M), *M. costatoides* (7.1-58 E; 7.2-19a M), *M. deltoidea* (7.1-40, 41, 57, 58 E; 7.2-19a M), *M. denuntiativa* (5.1-8 O), *M. eugenioides* (5.1-8 O), *M. minor* (5.1-17 M), *M. nitens* (7.1-58 E; 7.2-19a M), *M. obovata* (7.1-41 E), *M. prerostrata* (5.1-17 M), *M. reticulato-vernosa* (7.1-15, 41, 58 E; 7.2-14, 19a M), *M. rostrataformis* (7.1-98 E; 7.2-46 Pl), *M. santacruzensis* (7.1-8, 14 K; 7.2-5 M), *M. saraviana* (4.1-24 M), *Myrciaria acuminata* (7.1-58 E; 7.2-19a M), *M. tenuifolia* (7.2-30, 31 M), *Myrciophyllum ambiguaeoides* (7.1-58 E; 7.2-19a M), *Myrtaceidites* (7.1-50 O; 7.2-10, 43 M; see Other Angiosperms), *M. mesonesus* (7.1-19 K; 7.2-13 M; see citations under Other Angiosperms where original authors did not suggest family affinities), *M. verrucosus* (7.1-51, 52 O; 7.2-13 M), *Myrteola* (7.6-20 Q), *M. nummularia* (7.6-3 Q), *M. potosiana* (7.2-23, 25 Pl), *Myrtiphyllum bagualense* (7.1-15 O, 57 E), cf. *Psidium* (6.1-15 Pl/Pl–Q), *P. araciforme* (7.1-15, 41 E), *P. cuneatifolium* (7.2-46 Pl), *P. dissimile* (5.1-8 O), *P.* sp. (5.1-8 O), *P. membranaceum* (7.1-58 E; 7.2-19a M), *P. paulense* (7.1-98 E), *Psilasyncolporites* (7.2-45 M), *Syncolporites lisamae* (7.1-85 Pa–E; see also Other Angiosperms), *S. poricostatus* (7.2-50 M), *Tepualia stipularia* (7.6-12 Q).

Nelumbonaceae (see Nymphaeaceae).

Nyctaginaceae: *Allionia incarnata* (4.1-28, 29 Q), *Boerhavia wrightii* (4.1-28 Q), *Guapira* (7.6-32 Q), *Lymingtonia*? (7.2-10 M, Nyctaginaceae–Portulaceae; see also Other Angiosperms), *Mirabilis bigelovii* (4.1-28 Q), *Neea* (7.6-30, 31 Q), *Nyctaginites ellipticus* (7.1-41 E), *Pisonia* (7.6-31 Q), *P. branneri* (7.2-46 Pl), *P. conditi* (5.1-15, 16 M), *P. longifoliaformis* (5.1-17 M), *P. witti* (7.2-30 M).

Nymphaeaceae (7.2-39 Pl): *Echimonocolpites minutispinosus* (7.1-80 K, Nymphaeaceae?), *Nelumbo* (5.1-24 Q), *N. puertae* (leaves, associated fruits; Upper Cretaceous; Chubut, Patagonia, Argentina; Gandolfo & Cúneo, 2005), *Nymphaea* (5.1-23, 24 Q; 6.1-3 Q, 11 Q, 12 Q; 7.6-30 Q), *Paranymphaea aristolochiaformis* (7.1-28 Pa), *Parani[y]mphaea*? *patagonica* (7.1-15 E; see also Other Angiosperms).

Nyssaceae: *Nyssa* [?] (5.1-10 O).

Ochnaceae: *Gomphia firmifolia* (7.2-19a M), *Ouratea* (7.6-30–32 Q), *O. firmifolia* (7.1-41, 58 E), *O. guatemalensis* (6.1-18 Q).

Olacaceae: *Anacolosidites diffusa* (7.1-19 K, 29 Pa), *Liriosma* (6.1-18 Q).

Oleaceae (7.6-7 Q): *Forestiera* (4.1-25 M), *Fraxinus* (4.1-25 M, 32–34, 36 Q).

Onagraceae (4.1-29, 30, 33, 37 Q; 5.1-23 Q; 7.6-2, 20 Q): *Camissonia claviformis* (4.1-28 Q), *Corsinipollenites* (4.1-18 O/O–M; 5.1-7a E), *C. atlantica* (7.1-49, 52 O; 7.2-8 M), *C. exinitenuis* (7.2-13 M), *C. menendezii* (7.1-33, 37 Pa), *C. oculusnoctis* (7.2-43, 50 M, *Ludwigia*), *C. psilatus* (7.1-85 Pa–E, Onagraceae), *C. undulatus* (7.1-85 Pa–E, *Jussiaea* type), *Crassiorites australis* (7.1-47 E, *Fuchsia* type), *Diporites aspis* (7.1-51 O, *Fuchsia*; see also Other Angiosperms), *Epilobium* (7.6-20, 23 Q), *Fuchsia* (7.6-12, 20 Q), *F. regia* (7.6-32 Q), *Hauya* (5.1-10 O; 6.1-10 M/M–Pl), *Jussiaea* (6.1-18 Q), *Jussitriporites* (4.1-10 E; 7.1-66 E–O, 100 K), *J. mendendezii* (7.1-34, 35 Pa), *J.* cf. *undulatus* (4.1-22 M; 7.1-86 E), *Ludwigia* (4.1-26 Pl; 6.1-11 M/M–Pl; 7.2-39 Pl; 7.6-18, 20 Q), *Oenothera* (7.6-21, 23 Q), *O. multicaulis* (7.6-20 Q).

Orchidaceae (7.6-7 Q): *Orchideamasulites schlecteri* (7.2-43 M).

Orobanchaceae: *Orobanche cooperi* (4.1-28 Q).

Oxalidaceae (7.6-7 Q): *Oxalis* (5.1-10 O; 7.6-32 Q).

Palmae (4.1-18, 21 O/O–M, 39/40 Q; 5.1-20 M, 23 Q; 6.1-2 E, 2, 3, 5, 9 Q, 10, 11 M/M–Pl, 11 Q, 14, 15 Pl/Pl–Q, 17, 18, 20a, 22, 23 Q; 7.1-88 E [Palmae rays], 96 Pa; 7.2-27 Pl, 30 M, 39 Pl; 7.6-16, 20 Q): *Acoelorraphe wrightii* (5.1-23 Q), *Acrocomia* (5.1-23 Q), *Arecipites* (4.1-11 O/O–M; 5.1-7 E; 7.2-45 M), *A. columellus* (5.1-5 E), *A.* cf. *minutiscabratus* (7.1-51 O), *A. punctatus* (5.1-5 E), *A. regio* (7.1-85 Pa–E), *A. subverrucatus* (7.2-8 M; see also Other Angiosperms), *Astrocaryum* (4.1-26 Pl; 7.2-39 Pl), cf. *Attalea* (4.1-26 Pl; 6.1-9 M), *A. olssoni* (7.1-71 E), *Bactris pseudocuesco* (5.1-8 O), *Brahea* (4.1-25 M, 26 Pl), cf. *Chamaedorea* (4.1-26 Pl), *Clavamonocolpites* (7.2-50 M, *Iriartea*), C. *lorentei* (7.2-43 M), *Coccothrinax* (5.1-22 Q), *Colpothrinax wrightii* (5.1-23 Q), *Confertisulcites* (7.1-29 Pa), cf. *Cryosophila* (4.1-21 O/O–M; 6.1-7, 8 M/M–Pl), *Desmoncus* type (6.1-7 M), *Dictyocaryum* (7.6-14 Q), *Echidiporites barbeitoensis* (7.2-43 M), *Echimonocolpites franciscoi* (7.1-94 K, Pa, O–M), *Euterpe* (6.1-23 Q), *E.–Flagellaria schwageri* (a genus of Malpighiaceae; probably *Flagellaria*, Flagellariaceae; 7.2-19a M), *Geonoma* type (7.6-33 Q), *Iriartea* (6.1-18 Q), *I. collazoensis* (5.1-8 O), *Iriartites* (7.1-58 E), *I. restinensis* (7.1-71 E), *I. tumbezensis* (7.2-28a M), *I. vaughani* (6.1-3 M), *Liliacidites variegatus* (7.1-51 O; see also Other Angiosperms), *Longapertites microfoveolatus* (7.1-85 Pa–E, *Ereospatha*), *L. vaneendenburgi* (7.2-43 M, *Mauritia*, see also *Mauritidiites*), *Luminidites colombianensis* (7.1-85 Pa–E, *Phytelephas*), *Manicaria* type (6.1-7–9 M), *M. portoricensis* (5.1-8 O), *Mauritia* (7.6-20, 31 Q), *Mauritidiites* (5.1-7a E; 7.1-91 E), *M. franciscoi* (7.1-65 K–Pa, 84, 85 Pa–E, 87 E, 96 Pa; 7.2-43, 50 M; *Mauritia*), *Maximiliana* type (4.1-26 Pl), *Monocolpites medius* (7.1-87 E, 94 O–M), *Monocolpopollenites* (7.1-55 K), *Monosulcites* (7.2-45 M), *M. minutiscabratus* (7.1-19 K, 29 Pa), *Nypa pernambucensis* (7.1-97b Pa), palm rays (4.1-24 M; 7.1-88 E), *Palmacites* (7.2-32 M), *P. alius* (5.1-8 O), *P. berryanum* (see text, Costa Rica), *P. conformis* (5.1-8 O), *P. sparsistriatus* (5.1-8 O), *Palmaepollenites* (7.2-45 M), *Palmocarpon* (7.1-24 Pa), *P. acrocomioides* (5.1-8 O), *P. bactrioides* (7.2-44 M), *P. belensis* (7.1-70 E), *P. bravoi* (7.1-69, 70, 72 E), *P. cetera* (5.1-8 O), *P. cocoides* (7.1-70 E), *P.*

exemplare (5.1-8 O), *P. fusiforme* (7.2-44 M), *P. geonomoides* (6.1-4 Pl), *P. opinabile* (5.1-8 O), *P. rabellii* (5.1-8 O), *Palmophyllum* (5.1-8 O; 7.2-23, 25 Pl, 33, 44 M), *Palmoxylon* (7.1-24 Pa; see also Other Angiosperms), *P. palmacites* (6.1-6 M/M–Pl), *P. patagonium* (7.1-22 Pa), *Phytelephas* (6.1-18 Q), *Proxapertites* (4.1-22 M), *P. cursus* (7.1-85 Pa–E; 7.2-43 M), *P. minutus* (7.2-43 M), *P. operculatus* (7.1-29, 84, 85 Pa–E; 7.2-43 M; cf. *Astrocaryum*; see also Other Angiosperms), *P. verrucatus* (7.1-85 Pa–E), *Psilamonocolpites amazonicus* (7.2-50 M, *Euterpe*), *P. medius* (7.1-56, 84, 85 Pa–E, 94 K, Pa, O, M; 7.2-43 M; see Other Angiosperms), *P. rinconii* (7.2-50 M), *Racemonocolpites facilis* (7.1-85 Pa–E, *Iriartea* type; see also Other Angiosperms), *Raphia* (6.1-23 Q), *Retimonocolpites* (5.1-7a E), R. *longicolpatus* (7.2-43 M), R. *microreticulatus* (7.1-84 Pa), R. *regio* (7.1-84 Pa), R. *retifossulatus* (7.2-39 Pl, 43, 50 M), *Sabal ochseniusi* (7.1-58 E; 7.2-19a M), *S. parviflora* (5.1-23 Q), *Sabalites* (7.2-40 M), *Sabalpollenites* (7.1-29 Pa), *Socratea brownii* (4.1; see Poinar, 2002), *Spinozonocolpites* (7.1-29, 37 Pa, 91 E, *Nypa*; see also *Nypa*), *S.* aff. *baculatus* (7.1-85 Pa–E, *Nypa*), *S. echinatus* (7.2-43 M, *Nypa*, redeposited), *S. prominatus* (4.1-9 E, *Nypa fruticans*), *Synechanthus* type (6.1-7, 9 M), *Thrinax dominicana* (5.1-14; see Poinar, 2002), *T. radiata* (5.1-22 Q), *Trichotomosulcites* (7.2-43, 50 M, *Bactris*).

Pandanaceae: *Pandanas* (4.1-18 O/O–M), *Pandaniidites* (7.1-29 Pa), *P. texus* (7.1-31, 32, 37 Pa).

Papaveraceae (4.1-37 Q): cf. *Argemone* (4.1-33 Q), *Bocconia* (6.1-11 Q, 16 Q; 7.6-14 Q), *B. integrifolia* (7.6-20 Q), *Eschscholzia* (4.1-28 Q).

Passifloraceae: *Passiflora* (4.1-25 M, 26 Pl; 7.6-20, 30 Q), *P.* (?) *canfieldi* (7.2-22 M, 23, 25 Pl).

Pelliceriaceae (Pellicieraceae): *Lanagiopollis crassa* (7.1-85 Pa–E, *Pelliceria*), *Pelliceria* (*Pelliciera*) (4.1-20, 21 O/O–M, 23 M; 5.1-10 O; 6.1-2 E, 9 M, 14 Pl), *Pellicieroipollis* (4.1-11 E, 11 O/O–M; *Pelliceria*), *Psilatricolporites crassus* (4.1-11 O/O–M; 7.1-91 E; 7.2-43, 50 M, *Pelliceria*; see also Other Angiosperms).

Phytolaccaceae (4.1-33 Q): *Stegnosperma halimifolium* (4.1-28 Q).

Picrodendraceae: *Picrodendron macrocarpum* (5.1-23 Q).

Piperaceae (6.1-17 Q, 18 Q, 20–22 Q; 7.6-16, 30 Q): *Arthante geniculatoides* (7.1-15, 58 E; 7.2-19a, 30, 31 M), *Enckea columbrinoides* (7.2-30 M), cf. *Peperomia* (6.1-15 Pl/Pl–Q), *Piper* (7.6-32 Q), *Piperites cordatus* (6.1-5 Pl; 7.2-44 M), *P. potosiensis* (7.2-25 Pl), *P. quinquecostatus* (6.1-5 Pl).

Plantaginaceae: *Littorella australis* (7.6-12 Q), *Plantago* (4.1-29, 33, 34 Q; 7.6-2, 4, 6–8, 12, 13, 17, 20–23, 32 Q), *P. australis* (7.6-20, 32, 33 Q), *P. hispida* (7.6-11 Q), *P. insularis* (4.1-28 Q), *P. rigida* (7.6-15, 20 Q), *P. sericea* (7.6-20 Q), *P. turficola* (7.6-32, 33 Q).

Platanaceae: *Platanus* (4.1-18 O/O–M, 25 M), *P.* [?] *obtusiloba* (7.1-8 K), *P.* [?] *patagonica* (7.1-15 E).

Plumbaginaceae: *Armeria* (4.1-18 O/O–M), *A. maritima* (7.6-12 Q).

Poaceae (4.1-29 Q; see also Gramineae).

Podostemaceae (6.1-20a Q): *Tristicha* (6.1-18 Q).

Polemoniaceae (4.1-29 Q): *Gilia* (4.1-28 Q), *G.* cf. *glutinosa* (7.6-11 Q).

Polygalaceae (4.1-18 O/O–M; 6.1-18 Q; 7.6-31 Q): cf. *Bredemeyera* (4.1-26 Pl), *Monnina* (7.6-20, 21 Q), *Polygala* (4.1-30 Q; 7.6-4, 30, 32 Q), *Polygalacidites* (7.2-45 M), *Psilastephanocolporites fissilis* (7.1-85 Pa–E; 7.2-43, 50 M; see also Other Angiosperms), cf. *Securidaca* (4.1-26 Pl).

Polygonaceae (4.1-18 O/O–M, 32, 37 Q; 6.1-14, 15 Pl/Pl–Q, 17 Q): *Chorizanthe brevicornu* (4.1-28 Q), *C. commisuralis* (7.6-11 Q), *C. corrugata* (4.1-28 Q), *Coccoloba* (4.1-26 Pl; 6.1-2 E, 3, 11, 12, 18 Q), *C. ruizianiforma* (7.1-41 E), *Coccolobis preuvifera* (7.2-47 Pl), *C. tertiaria* (7.2-46 Pl), *Eriogonum* (4.1-30 Q), *E. fasciculatum* (4.1-28 Q), *E. wrightii* (4.1-28 Q), *Gymnopodium* (4.1-39/40 Q), *Muehlenbeckia* (7.6-20 Q), Polygonaceae cf. *Rumex–Ruprechtia* (7.6-13 Q), *Polygonum* (4.1-29, 30, 33 Q; 7.2-39 Pl; 7.6-7, 18, 20 Q), *P. bistortoides* type (6.1-11 Q, 18 Q), *Rumex* (6.1-2 Q, 11 Q; 7.6-2, 4, 7, 15, 21 Q), *R. tolimensis* (7.6-20 Q), *Ruprechtia braunii* (7.2-21 M, 23–25 Pl, 30 M), *R. castilloensis* (7.1-8 K), *R. latipedunculata* (7.1-48 E).

Pontederiaceae (4.1-18 O/O–M; 6.1-18 Q; 7.6-31 Q): *Eichornia* (4.1-39/40 Q; 7.6-33 Q), *E. crassipes* (5.1-23 Q), *Pontederia* (7.6-30 Q).

Portulacaceae (4.1-18 O/O–M, 29 Q; 6.1-18 Q; 7.6-23 Q): *Calandrinia* (7.6-8, 20 Q), *Cistanthe* (7.6-11 Q), *Lenzia* type (7.6-8 Q), *Montia* (7.6-22, 23 Q), *M. fontana* (7.6-20 Q), *M. meridensis* (7.6-20 Q).

Potaliaceae: *Desfontainia spinosa* (7.6-12 Q).

Potamogetonaceae: *Potamogeton* (4.1-29, 32, 33, 36, 39/40 Q; 5.1-24 Q; 6.1-3 Q, 15 Pl/Pl–Q; 7.6-15, 31 Q), *Potamogetonaceaepites* (7.1-50 O; cf. *Potamogeton pectinatus*), *Ruppia* (7.6-8, 24 Q).

Primulaceae (7.6-7 Q).

Proteaceae (4.1-39/40 Q; 6.1-11 Q; 7.1-60 E, 63 O [Proteaceae type?]; 7.6-16, 20, 23, 31 Q): *Echitriporites trianguliformis* (7.1-85 Pa–E, Proteaceae?; see also Other Angiosperms), *Embothriophyllum dubium* (7.1-38 E), *Embothrium coccineum* (7.6-2, 9, 12 Q), *E. precoccineum* (7.1-41 E), *E. pregrandiflorum* (7.1-41 E), *Euplassa* (7.6-31, 32 Q), *Lomatia* (7.6-7, 9, 12 Q), *L. bivascularis* (7.1-25–27 Pl), *L. occidentalis* (7.2-4 M), *L. patagonica* (7.2-4 M), *L. preferruginea* (7.1-41 E), *L.* cf. *serrulata* (7.1-15 E), *Lomatites occidentalis* (7.2-19b M), *Panopsis* (7.6-20 Q), *Propylipollis pseudocostatus* (7.1-85 Pa–E), *Proteacidites* (4.1-8 K; 7.2-10 M; see also Other Angiosperms), *P. crassus* (7.1-56 Pa), *P. dehaani* (7.2-43 M), *P. minor* (7.1-55 K), *P. obscurus* (7.1-51, 52 O), *P. parvus* (7.1-19 K), *P. triangulatus* (7.2-43 M), *Proteoxylon patagonicum* (7.1-54 K), *Retidiporites camachoi* (7.1-29 Pa), R. *magdalenensis* (7.1-85 Pa–E; see also Other Angiosperms), *Roupala* (7.6-31, 32 Q), R. *patagonica* (7.1-25–27 Pa), *Triatriopollenites lateflexus* (7.1-29 Pa; see also Other Angiosperms), *Tricolpites gillii* (7.1-45 E; see also Other Angiosperms).

Ranunculaceae (4.1-29, 33 Q; 7.6-2, 6, 7, 12, 13 Q): *Barneoudia* (7.6-12 Q), *Caltha* (7.6-3, 9, 12 Q), *Ranunculus* (6.1-16 Q; 7.2-39 Pl; 7.6-8, 20 Q), R. cf. *bonariensis* (7.6-32 Q), *Thalictrum* (4.1-26 Pl, 29, 32–34, 36 Q; 6.1-16 Q; 7.6-8, 17 Q), *T. podocarpum* (7.6-20 Q).

Restionaceae: *Leptocarpus chilensis* (7.6-12 Q), *Restioniidites* (7.1-37 Pa), R. *pascualii* (7.1-29 Pa).

Rhamnaceae: *Ceanothus* (4.1-25 M), *Colubrina* (4.1-25 M), *C. miocenica* (7.2-41, 44 M), *Condalia* (4.1-25 M; 7.6-7 Q), *Gouania* (5.1-23 Q), *G. firma* (7.2-32 M, 36 Pl), *G. membranacea* (7.2-32 M, 36 Pl), *G. miocenica* (4.1-24 M), cf. *Karwinskia* (6.1-15 Pl/Pl–Q), *K. axamilpense* (4.1-16 O/O–M), *Reynosia latifolioides* (5.1-17 M), *Rhamnidium elaeocarpoides* (7.2-30 M), R. *miocenicum* (7.2-44 M), R. (?) *patagonicum* (7.2-19b M), R. *preglabrum* (7.2-19b M), *Rhamniphyllum casearifformis* (7.1-98 E), *Rhamnus* (4.1-25 M; 7.6-32 Q), R. *fortinervosus* (7.1-15 E), R. *sanctaeflaviaensis* (7.1-15 E), R. sp. (7.1-15 E), *Zizyphus* (7.1-57 E; 7.6-30 Q), *Z. chubutensis* (7.1-28 Pa), *Z. elliptica* (5.1-17 M), *Z. minor* (5.1-17 M), *Z. pseudochloroxylon* (5.1-8 O).

Rhizophoraceae: *Cassipourea* (6.1-18 Q), *Rhizophora* (4.1-20, 21 O/O–M, 23 M, 26 Pl, 38, 39/40 Q; 5.1-10 O; 6.1-2 E, 7–10 M, 12, 13 Pl, 18 Q; 7.1-94 O–M, 96 E; 7.6-28 Q), R. *boweni* (7.2-40 M), R. (?) *doctrinalis* (5.1-8 O), R. *mangle* (5.1-23 Q; 7.6-26 Q), *Rhizophoroxylon spallettii* (7.1-24 Pa), *Verrutricolporites rotundiporus* (7.2-50 M, *Rhizophora*), *Zonocostites* (4.1-11 E, O/O–M), *Z. duquei* (7.2-50 M, *Rhizophora*), *Z. ramonae* (7.1-66 E–O, 100 Paleogene; 7.2-43 M, *Rhizophora*).

Rosaceae (4.1-18 O/O–M, 29, 30, 33 Q; 6.1-11 Q, 16 Q; 7.6-4, 7, 20 Q): *Acaena–Polylepis* (7.6-2, 8, 12, 13, 15, 17, 20–23 Q), *Cercocarpus* (4.1-25 M), *C. mixteca* (4.1-14 O/O–M), *Chilechicoxylon microporosum* (7.1-54 K, Rosaceae? Paleogene?), *Chrysobalanus precuspidatus* (7.2-46 Pl), *C. preicaco* (7.2-46 Pl), *Citrophyllum bahiensis* (7.2-46 Pl), *Crossosoma* (4.1-25 M; Crossosomataceae), *Hirtella lojana* (7.2-30 M), *Holodiscus* (4.1-25 M), *Laurocera sus* (4.1-25 M), *Lyonothamnus* (4.1-25 M), *Moquilea stubeli* (7.2-32 M, 36 Pl), *Osteomeles pliocenica* (7.2-24, 25 Pl), *Pilocarpus prepinnatifolius* (7.2-46 Pl), *Polylepis prenuntia* (7.1-41 E), *Prunus* (4.1-25 M; 7.6-32 Q), *Rubus* (7.2-39 Pl), *Sericotheca argentea* (7.6-20 Q).

Rubiaceae (4.1-29, 37 Q; 6.1-2 Q, 9 M, 16–18 Q; 7.2-39 Pl; 7.6-2, 4, 6, 7, 12, 20, 30, 32 Q): cf. *Alibertia* (4.1-26 Pl), *Borreria* (4.1-26 Pl; 5.1-23 Q; 6.1-11 Q, 18 Q; 7.6-13, 18, 29, 30, 32 Q), *B. anthospermoides* (7.6-20 Q), *B. laevis* (7.6-20 Q), *B.* cf. *latifolia* (7.6-32 Q), *Bothriospora witti* (7.2-32 M, 36 Pl), *Canthiumidites* aff. *bellus* (7.1-51 O; *Gardenia* [?, presently Paleotropical]; see also Other Angiosperms), *Cephalanthus glabratifolius* (7.1-41 E), *Chiococca* (4.1-25 M), *Chomelia* (6.1-10 M), *Condaminea grandifolia* (7.2-28a M), *Coprosma incerta* (7.1-41 E), *C. spathulatifolia* (7.1-41 E), *Cosmibuena* (6.1-10 M), *Coussarea membranacea* (7.1-58 E; 7.2-19a M), *C. tertiaria* (7.1-41 E), *Endlicheria rhamnoides* (7.2-31 M), *Exostema precaribaeum* (5.1-17 M; 7.2-30 M), *Faramea* (4.1-26 Pl; 5.1-10 O; 6.1-2 E, 10 M, 18 Q), *F. miocenica* (7.2-19b M), *F. occidentalis* (5.1-23 Q), *Galium* (4.1-29 Q; 7.6-11 Q), *G. stellatum* (4.1-28 Q), *Gouatteria tenuinervis* (7.1-58 E; 7.2-19a M), *Guettarda calyptrata* (5.1-23 Q), *G. cookei* (4.1-24 M; 5.1-15, 16 M), *G. intercalaris* (5.1-8 O), *Hoffmannia boliviana* (7.2-25 Pl), *H. protogaea* (7.1-41, 58 E; 7.2-19a M), *Machaonia* (7.6-25 Q), *Posoqueria* (6.1-10 M), *P. columbiana* (7.2-30, 32, 33 M), *Psilatricolpites comprosmoides* (7.1-56 Pa, *Coprosma*), *Psilatriporites corstanjei* (7.2-50 M, *Faramea*?), cf. *Psychotria* (7.2-39 Pl; 7.6-32 Q), *P.* cf. *alba* (7.6-32 Q), *P. eogenica* (7.1-70 E), *P. grandifolia* (7.1-58 E; 7.2-19a M), *Randia* (6.1-18 Q), *Relbunium* (7.6-20, 32 Q), *Remijia tenuiflorifolia* (7.1-41 E), *Retitricolporites crassicostatus* (7.2-50 M), *Rondeletia* (?; 4.1-24 M), R. *goldmani* (6.1-6 M), R. *longiflorifolia* (7.1-41 E), *Rubiacites chomeliifolia* (7.1-41 E), R. *ixoreoides* (6.1-6 M), R. *nummularioides* (7.2-23–25 Pl), *Sabicea* (6.1-7 M, 14 Pl), *S. asperifolia* (7.2-32 M), *S.* (?) *elliptica* (7.1-58 E; 7.2-19a M), *Terebraria* (4.1-26 Pl), *Uragoga tertiaria* (7.1-70 E), *Warszewiczia* (7.6-20 Q).

Ruppiaceae: *Ruppia maritima* (4.1-32 Q).

Rutaceae (4.1-18 O/O–M; 6.1-11 Q; 7.6-30 Q): *Casimiroa* (6.1-10 M), *Citrus* type (6.1-3 Q), *Condaminea grandifolia* (7.2-32 M, 36 Pl), *Cusparia yacuibana* (7.2-26 Pl), *Erythrochy[i]ton bahiense* (7.2-46, 47 Pl), *E. borrelloensis* (7.1-15 E), *E. grandifolium* (7.1-58 E; 7.2-19a M), *Euxylophoroxylon chiquichanense* (7.1-24 Pa), *Fagara dentatafolia* (7.2-46 Pl), *F. formosa* (7.2-46 Pl), *F. miocenica* (5.1-17 M; 7.2-44 M), *F. piurana* (7.1-70 E), *F. serrata* (7.1-41 E), *F. wadii* (4.1-24 M), *Pilocarpus saavedrai* (7.1-58 E; 7.2-19a M), *Rhoipites* cf. *baculatus* (7.1-50 O, *Ruta*), R. sp. A (7.1-34, 35, 37 Pa; *Ruta*; see also Other Angiosperms), Rutaceae–*Esenbeckia* (7.6-30 Q), *Ticorea foetidoides* (7.1-58 E; 7.2-19a M), *Zanthoxylum* (6.1-3 Q, 17 Q; 7.2-14 M, 39 Pl; 7.6-18, 30, 32 Q), *Z. inaequabile* (7.1-58 E; 7.2-19a M), *Z. glanduliferum* (7.1-98 E), *Z. panamensis* (?) (6.1-18 Q), *Z. setulosum* (6.1-18 Q), *Z. tenuifolium* (7.1-58 E; 7.2-19a M).

Sabiaceae: *Meliosma* (4.1-26 Pl; 7.6-32 Q).

Salicaceae (7.6-7 Q): *Populus* (4.1-25 M, 26 Pl), *P.* cf. *microphylla* (7.1-8 K), *P.* [?] cf. *nebrascensis* (7.1-8 K), *Salix* (4.1-25 M, 31, 32, 34, 36, 37 Q; 5.1-10 O; 6.1-11 Q, 15 Pl/Pl–Q), *S.* [?] *proteaefolia* (7.1-8 K).

Santalaceae: *Antidaphne lotensis* (Eremolepidaceae; 7.2-19a M), *Nanodea muscosa* (7.6-2, 12 Q), *Quinchamalium* (7.6-12 Q).

Sapindaceae (4.1-18 O/O–M; 6.1-2 Q, 11 Q, 21 Q; 7.1-61 E [Sapindaceae type, age uncertain]; 7.6-30 Q): *Allophylus* (4.1-26 Pl; 5.1-20 M, 23 Q; 6.1-7, 10 M; 7.6-32 Q), *A. eduliformis* (7.1-41 E), *A. graciliformis* (7.1-15, 41 E), *Cardiospermum* (4.1-25 M; 6.1-2 E; 7.6-20 Q), *Cupania* (4.1-26 Pl; 6.1-7, 10 M, 18 Q), *C. cordinii* (7.1-41 E), *C. grosse-serrata* (7.1-15, 41 E; 7.2-19b M), *C. inserta* (7.2-19b M), *C. latifolioides* (7.1-15, 41 E; 7.2-19b M), *C. patagonica* (7.1-15, 41 E), *C. romeroi* (7.1-57 E), *C. vernaliformis* (7.1-15, 41, 57 E), *C.* sp. (7.1-15 E), *Cupanieidites* (5.1-7a E), *C. peruvianus* (7.1-69 E), *C. reticularis* (7.1-51, 52 O, 56 Pa; see also Other Angiosperms), *Cupanoides peruvianus* (7.1-70 E), *Diatenopteryx fossilis* (7.1-41 E), *D. sorbifoliiforma* (7.1-41 E), *Dodonaea* (4.1-25 M, 33, 34 Q; 7.6-8, 15, 17, 23 Q), *D. arborea* (6.1-11 Q), *D. cubensis* (5.1-17 M), *D. vera* (7.2-46 Pl), *D. viscosa* (7.6-20 Q), *D. viscosaformis* (7.2-24, 25 Pl), *Matayba* (4.1-

26 Pl; 6.1-7 M), *M. belensis* (7.1-70 E), *M. marginatifolia* (7.1-15 Pa, E, 41 E), *Melicoccus immutata* (5.1-8 O), *M.* sp. (5.1-8 O), *Paullinia* (4.1-26 Pl; 6.1-2 E, 10 M, 18 Q), *P. prerufescens* (7.1-41 E), *P. rubiginosifolia* (7.1-41 E), *Sapindoides peruvianus* (7.1-69, 70, 72 E), *Sapindoxylon antioquiense* (7.1-78c O–M; 7.2-35 O–M), *Sapindus* (4.1-25 M; 5.1-24 Q), *S. acuminatus* (7.1-58 E; 7.2-19a M), *S. argentinus* (7.1-41 E; 7.2-19b M), *S. brittonii* (5.1-8 O), *S. gracilentus* (5.1-8 O), *S. hispaniolana* (5.1-15 M), *S. obesus* (5.1-8), *S. presaponaria* (5.1-17 M; 7.2-46, 47 Pl), *S. pseudomarginatus* (5.1-8 O), *Schmidelia bejucensis* (6.1-6 M/M–Pl), *S. eduliforma* (7.2-19b M), *S. graciliforma* (7.2-19b M), *S. proedulis* (7.2-19b M), *Serjania* (6.1-2 E, 10 M; 7.6-30, 32 Q), *S. itaquaquecetubensis* (7.1-98 E), *S. lancifolia* (7.1-98 E), *S. tertiaria* (7.2-30 M), *Syncolporites anibalii* (7.2-50 M), *Talisia ecuadoriana* (7.2-30 M), *Thouinia* (4.1-25 M), *T. philippii* (7.1-58 E; 7.2-19a M), *Urvillea* (7.6-20, 32 Q).

Sapotaceae (4.1-18 O/O–M, 22 Pl, 39/40 Q; 5.1-23, 24 Q; 6.1-3 Q, 5 Q, 6 Q, 12 Q, 14 Q, 15 Pl/Pl–Q, 17 Q, 19 Q; 7.1-94 O–M, 96 E): *Achras* (6.1-3 Q), cf. *Bumelia* (6.1-10 M/M–Pl), *B. australis* (7.1-41 E), *B. cunaetafolia* (5.1-16 M), *B. cuneatoides* (7.2-46 Pl), *B. lojana* (7.2-30 M), *B. marahiana* (7.2-46 Pl), *B. reclinatafolia* (5.1-15 M), *B. retusafolia* (5.1-17 M), *B. trinitense* (7.2-44 M), *Chrysophyllum* (5.1-10 O; 6.1-2 E; 7.1-15 E; 7.6-32 Q), *C. cahobasensis* (5.1-16 M), *C. cainitoformis* (7.2-42 M), *C. comparabile* (5.1-8 O), *C. marginatum* (7.6-32 Q), *C. preoliviforme* (7.1-89 E), *C. pseudargenteum* (5.1-8 O), *C. pseudargenteum* var. *oblongum* (5.1-8 O), *C. rufoides* (7.2-32 M, 36 Pl), *Dipholis pseudoleiantha* (5.1-8 O), *Ecclinusa* (7.2-39 Pl), *Labatia fonsecana* (7.2-47 Pl), *Mimusops anomala* (7.2-44 M), *M. emarginata* (5.1-21 Q), *M. leonii* (5.1-17 M), *M. miocenica* (5.1-17 M; 7.2-30, 42, 44 M), *M. praeparvifolia* (5.1-16 M), *M. preduplicata* (7.6-26 Q), *Pouteria* (7.6-30 Q), cf. *Pouteria* (6.1-7 M/M–Pl), *Pouterlabatia clarki* (7.1-15, 41 E), *P. lanceolata* (7.1-15, 41 E), *Psilastephanocolporites marinamensis* (7.2-50 M), *Psilatricolporites divusus* (7.2-50 M), *P. labiatus* (7.2-50 M), *P. maculosus* (7.2-43 M, *Chrysophyllum*), *P. transversalis* (7.2-43 M), *Sapota agnitionalis* (5.1-8 O), *Sapotaccoidaepollenites* (7.2-45 M), *Sideroxylon aequale* (5.1-8 O), *S. mastichodendroides* (7.2-41, 44 M), *Tetracolporopollenites maculosus* (7.1-85 Pa–E, *Chrysophyllum*).

Saxifragaceae (see also Grossulariaceae, Hydrangeaceae, Verbenaceae): *Escallonia frenguellii* (7.1-15 E), *E. wendtii* (7.2-22 M, 23, 25 Pl), *Hydrangea? incerta* (7.1-15, 41 E).

Scrophulariaceae (4.1-18 O/O–M, 37 Q; 7.6-7 Q): *Aragoa* (7.6-20 Q), *Calceolaria* (7.6-20 Q), *Euphrasia* (7.6-9, 12 Q), *Galvezia juncea* (4.1-28 Q), *Tricolpites trioblatus* (7.2-13 M; see also Other Angiosperms).

Simaroubaceae: *Castela* (7.6-25 Q), *Quassia* (6.1-18 Q), *Simaruba* (7.6-30 Q; *Quassia*), *S. glaucaformis* (5.1-17 M), *S. haitensis* (5.1-16 M), *S. miocenica* (7.2-40 M), *S. veracruziana* (4.1-24 M), *S. versicoloroides* (7.1-77 E), *S. whitei* (7.2-46 Pl).

Smilacaceae: *Smilacipites saltensis* (7.1-50 O–M, *Smilax*), *Smilax* (4.1-26 Pl; 7.6-31 Q).

Simmondsiaceae: *Simmondsia chinensis* (4.1-28 Q; Buxaceae).

Siparunaceae (see Monimiaceae).

Solanaceae (4.1-18 O/O–M, 30, 33 Q; 5.1-24 Q; 6.1-2 Q, 11 Q, 16 Q, 17 Q; 7.2-39 Pl; 7.6-4, 6–8, 13, 20, 30, 31 Q): *Acnistus* (7.6-18 Q), *Brugmansia* (*Datura*, *Methysticodendron*; 7.6-20 Q), *Exodeconus integrifolius* (7.6-11 Q), *Fabiana* (7.6-11 Q), *Lycium* (4.1-28 Q), *Lycopersicon chilense* (7.6-11 Q), *Nicotiana* (4.1-28 Q), *N. trigonophylla* (4.1-28 Q), *Physalis* (4.1-28 Q), *Salpichroa* type (7.6-8 Q), *Sessea* (7.6-20 Q), *Solanum* (6.1-3 Q, 6 Q, 12 Q; 7.6-8, 32 Q), *S. hindsianum* (4.1-28 Q), *Trechonaetes* (7.6-8 Q).

Sparganiaceae: *Sparganiaceaepollenites* (see also Other Angiosperms) *barungensis* (7.1-49–52 O; 7.2-8, 13 M; see also Other Angiosperms), *Sparganium* type (6.1-11 Q).

Staphyleaceae: *Turpinia* (7.2-39 Pl).

Sterculiaceae (see also Bombacaceae, Tiliaceae): *Ayenia* (4.1-23 M; 7.6-20 Q), *Bue(y)ttneria* (4.1-26 Pl; 6.1-18 Q; 7.2-33 M), *B. asterotrichiformis* (7.1-15, 41 E), *B. cinnamomifolia* (6.1-5; 7.2-32 M, 36 Pl), *B. lanceolatifolia* (7.1-15, 41 E), *Fremontodendron* (4.1-25 M), cf. *Guazuma* (6.1-7 M; 7.1-15 E), *G. tertiaria* (7.2-28b M), *Helicteres* (7.6-31 Q), *Melochia carrioni* (7.2-30 M), *Reevesia* (4.1-18 O/O–M), *Retitricolporites guianensis* (7.2-43 M), *Rhoipites guianensis* (7.1-85 Pa–E, Sterculiaceae–Malvaceae), *Sterculia acuminataloba* (7.1-28 Pa), *S. guinazui* (7.1-15, 41 E), *S. patagonica* (7.1-8 K, 41 E; 7.2-19b M), *S. sehuensis* (7.1-8, 14 K), *S. washburni* (7.1-8 K, 15, 41 E), *Theobroma tertiaria* (7.2-42 M), *Tiliapollenites danei* (4.1-11 E, O/O–M; Bombacaceae–[probably Sterculiaceae]–Tiliaceae).

Strychnaceae (see also Loganiaceae): cf. *Strychnos* (6.1-15 Pl/Pl–Q).

Styracaceae: *Styrax* (7.6-31, 32 Q), *S. acuminatiformis* (7.1-41 E; 7.2-19b M), *S. coriacea* (7.1-15, 58 E; 7.2-19a M), *S. glabratoides* (7.1-15, 58 E; 7.2-19a M), *S. glandulifera* (7.1-15, 41 E), *S. lanceolata* (7.2-28a, 32 M, 36 Pl), *S. lehneri* (7.2-42, 44 M), *S. preferrugineum* (7.2-46 Pl), *S. rosadoi* (7.6-27 Q), *S. styracioides* (7.2-30 M).

Symplocaceae: *Antholithus venezuelensis* (7.2-40 M), *Senipites patagonica* (7.1-51, 52 O; 7.2-8, 10 M; *Symplocos*), *S. tercrassata* (7.1-29 Pa; *Symplocos?*), *Symplocos* (6.1-10 M, 15 Pl/Pl–Q, 16 Q, 18 Q; 7.2-39 Pl; 7.6-20, 31 Q), *S. commutatifolia* (7.1-41 E), *S. lanceolata* type (7.6-32 Q), *S. limoncillo* (6.1-15 Pl/Pl–Q), *S. tenuifolia* type (7.6-32 Q).

Theaceae: *Cleyera* (4.1-26 Pl), *Freziera* (7.2-39 Pl), *Laplacea* (7.6-31 Q), *L. fruticosa* (7.6-32 Q).

Thymelaeaceae: *Drapetes muscosus* (7.6-9, 12 Q), *Daphnopsis* (4.1-26 Pl; 5.1-23 Q; 7.6-20 Q), *D.* cf. *beta* (7.6-6 Q), *Ovidia* (7.2-16 M; 7.6-12 Q).

Tiliaceae (4.1-18 O/O–M; 6.1-11 Q; 7.6-16, 20 Q; see also Bombacaceae, Sterculiaceae): *Apeiba* (6.1-18 Q), *Corchorus* (5.1-23 Q; 6.1-11 Q), *Heliocarpus* (4.1-18 O/O–M; 6.1-6 Q, 13 Q, 14 Q; 7.6-20, 25 Q), *Luehea* (6.1-3 Q, 11 Q; 7.6-30, 32 Q), *L. divaricatiformis* (7.1-98 E), *L. seemannii* (6.1-18 Q), *L. tertiaria* (7.2-30, 31 M), *Mortoniodendron* (4.1-26 Pl; 6.1-2 E, 10 M), *Quercoidites* (7.2-45 M), *Tilia* (4.1-36 Q), *Tiliaepollenites* (see also

Other Angiosperms) *notabilis* (7.1-56 Pa; Tiliaceae?, *Tilia*?), *Triumfetta irregulariter-serrata* (7.1-15, 41, 58 E; 7.2-19a M), *T. miocenica* (7.1-58 E).

Trigoniaceae: *Trigonia* (7.6-32 Q), *T. varians* (7.2-28a, 30, 32 M, 36 Pl, 40, 42 M).

Typhaceae: *Typha* (4.1-18 O/O–M, 25 M, 29–32, 35, 36, 39/40 Q; 5.1-23, 24 Q; 6.1-1–3 Q, 8 Q, 18 Q, 19 Q, 21 Q; 7.6-6, 7, 20, 25, 31 Q), *T. angustifolia* (7.6-8, 24 Q), *T. domingensis* (5.1-23 Q; 7.6-32 Q).

Ulmaceae (4.1-18 O/O–M; 6.1-3 Q; 7.6-20 Q): *Cedrelospermum manchesteri* (4.1-13 O/O–M), *Celtis* (4.1-25 M, 26 Pl, 33, 37, 39/40 Q; 5.1-24 Q; 6.1-1–3 Q, 6 Q, 9–14 Q, 15 Pl/Pl–Q, 17 Q; 7.6-7, 14, 20, 24, 29–33 Q), *C. ameghinoi* (7.1-41 E; 7.2-19b M), *C. bolivarensis* (7.1-76 E), *Celtis*–Moraceae (4.1-30 Q), *Chaetoptelea* (4.1-39/40 Q; 6.1-3 Q, 5 Q, 6 Q, 9 Q, 13 Q, 14 Q), *Lozanella*, *Trema* (7.6-15 Q), *Magdalenophyllum aequilaterum* (4.1-13 O/O–M), *Momisia* (7.1-15 E), *M. asperulaformis* (7.2-28b M), *M. australis* (7.1-41 E), *M. ecuadorensis* (7.2-30 M), *M. iguanaeaformis* (7.2-28b, 30 M), *Phyllostylon* (4.1-39/40 Q; 5.1-24 Q), *Tetrapollis* (7.2-45 M), *Trema* (4.1-39/40 Q; 5.1-23, 24 Q; 6.1-1 Q, 3 Q, 5 Q, 6 Q, 10–12 Q, 14 Q, 20–22 Q; 7.6-14, 24, 25, 32 Q), *T. floridana* (6.1-12 Q), *T. micranthaformis* (7.2-28b M), cf. *Trema–Lozanella* (7.6-15 Q), *Ulmoideipites krempii* (7.1-85 Pa–E; see also Other Angiosperms), *U. patagonicus* (7.1-29 Pa), *Ulmus* (4.1-26 Pl, 32, 33, 39/40 Q; 6.1-11 M/M–Pl, 11 Q, 12, 15 Pl/Pl–Q, 16 Q), *Verrustephanoporites simplex* (7.1-19 K, 31, 32, 37 Pa; *Phyllostylon*; see also Other Angiosperms).

Umbelliferae (4.1-30, 32, 33, 37 Q; 5.1-23 Q; 6.1-15–17 Q, 21 Q; 7.6-2, 3, 6–9, 12, 13, 15, 17, 20, 21, 23, 30–33 Q): *Apium* type (7.6-8, 32 Q), *Azorella* (7.6-4, 8, 20 Q), *Daucus* type (7.6-6 Q), *Eryngium* (4.1-29, 34, 37 Q; 7.6-32, 33 Q), *Hydrocotyle* (4.1-29, 33 Q; 7.6-15, 20, 32, 33 Q), *Mulinum* type (7.6-4, 8 Q).

Urticaceae (Urticaceae–Moraceae) (4.1-18 O/O–M, 29, 33, 34 Q; 6.1-11 Q, 20–22 Q; 7.6-6–8, 30, 32 Q; see also Moraceae, Urticales): *Cecropia* (4.1-39/40 Q; 5.1-24 Q; 6.1-1 Q, 2 Q, 9 Q, 11 Q, 16 Q, 19–22 Q; 7.2-39 Pl; 7.6-14, 16, 20, 21, 24, 25, 28–30, 32 Q; Cecropiaceae), *Coussapoa* (7.2-39 Pl; Cecropiaceae), *C. prepliocenica* (7.1-15 O), *C. quinquenervis* (7.2-19a M), *C. veracruziana* (4.1-24 M), *C. villosoides* (7.2-40 M), *Parietaria hespera* (4.1-28 Q), *Pilea* (5.1-24 Q; 6.1-20–22 Q; 7.6-20 Q), *Urtica* (7.2-39 Pl).

Urticales (4.1-39/40 Q; 6.1-1, 16, 18 Q; 7.6-15, 17, 22, 23 Q; see also Moraceae, Urticaceae).

Valerianaceae (7.6-32 Q): *Valeriana* (4.1-33 Q; 6.1-16 Q; 7.6-2, 9, 12, 13, 15, 17, 20, 21, 23 Q), *V. arborea* type (7.6-20 Q), *V. stenophylla* type (7.6-20 Q), *V. triphylla* type (7.6-20 Q).

Velloziaceae: *Vellozia* (7.6-30, 31 Q).

Verbenaceae (7.6-4, 6, 8 Q): *Acantholippia deserticola* (7.6-11 Q), *Aegiphila* (6.1-10 M), *Avicennia miocenica* (7.2-33 M), *A. nitida* (7.6-26 Q), *Citharexylon retiformis* (7.2-32 M, 36 Pl), *Donatia* (*Avicennia*) *fascicularis* (7.6-3, 12 Q; Saxifragaceae), *Junellia seriphioides* (7.6-11 Q), *Lippia* (4.1-25 M), *Petrea* (6.1-10 M), *Retitricolporites* (7.2-43 M, *Avicennia*), *Rhaphithamnus spinosus* (7.6-12 Q), *Verbena* (4.1-28 Q; 7.6-32 Q).

Violaceae: *Corynostylis* (5.1-10 O), *Tricolpites asperamarginis* (7.1-51 O, Violaceae?), *Viola* (7.6-20 Q).

Vitaceae (6.1-11 Q; see also Leeaceae): *Ampelocissus bravoi* (7.1-70 E), *Cissites patagonica* (7.1-28 Pa), *Cissus* (5.1-23 Q; 6.1-18 Q), *C. pichileufensis* (7.1-41 E; 7.2-14 O–M), *C. striata* (7.6-12 Q), *C. willardi* (7.1-70 E), *Vitis* (4.1-25 M; 6.1-3 Q).

Vochysiaceae: *Vochysia* (6.1-18 Q), *V. acuminatafolia* (7.2-46 Pl), *V. dura* (7.1-58 E; 7.2-19a M), *V. ferruginoides* (7.2-30, 31 M), *V. retusifolia* (7.2-28a, 32 M, 36 Pl), *V. witti* (7.2-31 M).

Winteraceae: *Drimys* (6.1-15 Q, 16 Q), *D. brasiliensis* (7.6-20 Q), *D. granadensis* (7.6-20 Q), *D. patagonica* (7.1-41 E), *D. winteri* (7.6-2, 3, 9, 12 Q), *Pseudowinterapollis couperi* (7.1-46 E, 51, 52 O; *Drimys*?; see also Other Angiosperms).

Xyridaceae: *Xyris* (7.2-39 Pl; 7.6-32, 33 Q).

Zingiberaceae: *Costus* (?) *incertus* (7.2-44 M).

Zygophyllaceae: *Fagonia pachyacantha* (4.1-28 Q), *Guaiacum pliocenicum* (7.2-46 Pl), *Kallstroemia* (4.1-28 Q), *Larrea divaricata* (4.1-28 Q), *Porlieria tertiaria* (7.2-22 M, 23, 25 Pl), *Tribulus* (5.1-23 Q; 7.6-25 Q).

Other angiosperms/Incertae sedis/Position unknown (depending on author)

Acaciapollenites myriosporites (7.1-52 O; see also Leguminosae), *Acacioxylon* (4.1-41 Tertiary undifferentiated; see also Leguminosae), *Aesculiidites* (7.1-66 E–O), *Afropollis jardinus* (7.1-78d K), *Aglaroeidia*? *foveolata* (7.1-85 Pa–E), *Ailanthipites* (7.1-19 K, 31, 32 Pa; see also Anacardiaceae), *Alaticolpites limai* (7.1-99, 100 K), *Albertipollenites angululuminosus* (7.1-29 Pa), *A.* (?) *perforatus* (7.1-85 Pa–E), *Alnipollenites* (4.1-10 E), *Anacolosidites* (7.1-16 K), *A.* cf. *luteoides* (7.1-100 K; 7.2-43 M), angiosperm leaves (unidentified; 7.1-4 K), *Annutriporites iversenii* (7.1-86 E), *Apoci[y]nophyllum chalianum* (7.1-8 K; see also Apocynaceae), *Applanopsis dampieri* (7.1-100 K), *Aquilapollenites* (4.1-8 K), *A. magnus* (7.1-100 K), *Aralaephyllum cachetamanense* (7.1-8 K), *Araliaceoipollenites* (7.1-85 Pa–E), *Arapipia florifera* (7.1-97a K), *Arcotriporites asteroides* (7.1-86 E), *Arecipites subverrucatus* (7.1-49, 52 O; see also Palmae), *Asterisporites asteroides* (7.1-3 K), *Auriculiidites reticulatus* (7.1-67, 68, 100 K), *Baculamonocolpites hammenii* (7.1-85 Pa–E), *B. minimus* (7.1-80 K), *B. multispinosus* (7.1-80–82 K), *Baculamorphomonocolpites tausae* (7.1-80–82 K, 85 Pa–E), *Baculatisporites multibaculae* (7.1-81 K), *Bacustephanocolpites stereos* (7.1-86 E), *Bacutriporites echinatus* (7.1-85 Pa–E), *Bahiaporites reticularis* (7.1-100 K), *Basopollis krutz[s]chi* (5.1-6 E), *B.–Brosipollis* cf. *striata–Choanopollenites* (5.1-7 E), *Baumannipollis variaperturatus* (7.1-49 O; see also Malvaceae), *Beaupreaidites* (7.1-55 K), *Bignonites chalianum* (7.1-8 K; see also Bignoniaceae), *Bombacacidites annaeoides* (7.1-95 Pa; see also Bombacaceae), *Brevitricolpites macroexinatus* (7.1-85 Pa–E), *B. microechinatus* (7.1-85 Pa–E), *B. variabilis* (7.1-86 E), *Buttinia andreevi* (7.1-100 K), *Bysmapollis verrucosus* (7.1-44 E), *Callistopollenites* (7.1-30 Pa), *Canthiumidites* aff. *bellus* (7.1-52 O; see also Rubiaceae),

Caryophyllidites polyporatus (7.1-56 Pa), *Castaneapollenites* (4.1-11 O/O–M), *Chenopodipollis* (4.1-10 E; see also Chenopodiaceae [chenoam]), *C. chenopodiaceoides* (7.1-49, 52 O; see also Chenopodiaceae [chenoam]), *Circulina parva* (5.1-2 K), *Cissites parvifolius* (7.1-8 K), *Clatonipollenites*? (7.1-100 K), *Clavainaperturites clavatus* (7.1-94 O–M; 7.2-43 M; see also Chloranthaceae), *Clavamonocolpites* (7.1-85 Pa–E), *C. terrificus* (7.1-86 E), *Clavastephanocolpites crotonoides* (7.1-94 E), *Clavastephanocolporites ambigens* (7.1-95 Pa), *Clavatipollenites* (7.1-5, 10 K, 49, 52 O, 99, 100 K), *C. hughesii* (7.1-3, 55 K), *Clavatricolpites annemariae* (7.1-94 E), *C. densiclavatus* (7.1-85 Pa–E), *C. gracilis* (7.1-31, 32, 37 Pa, 86 E), *Clavatricolporites guianensis* (7.1-95 Pa), *C. leticiae* (7.1-94, 95 Pa; 7.2-43 M), *Colombipollis tropicalis* (7.1-85 Pa–E), *Complexipollis abditus* (4.1-8 K), *Concolpites leptos* (7.1-45 E), *Crassiectoapertites columbianus* (7.2-43 M), *Crassitricolporites brasiliensis* (7.1-100 K), *Cretaceioporites polygonalis* (7.1-78d K), *Cricotriporites almadensis* (7.1-100 K), *C. elongatoporus* (7.1-85 Pa–E), *C. guianensis* (7.1-33 Pa, 85 Pa–E, 95 Pa, 100 K; 7.2-13, 50 M), *C. macroporus* (7.1-85 Pa–E), *C. minutiporus* (7.1-85 Pa), *C. operculatus* (7.1-100 K), *Cristatricolpites analemae* (7.1-95 Pa), *Crototricolpites americanus* (7.1-96 Pa), *C. annemariae* (7.1-85 Pa–E, 95 Pa, 100 K; 7.2-43 M), *C. protoannemariae* (7.1-85 Pa–E), *Crusafontites grandiosus* (7.1-81, 82 K), *C. megagemmatus* (7.1-85 Pa–E), *Cupaniedites* (7.1-59 E, 64 E–O), *C. reticularis* (7.1-49 O, 100 K; see also Sapotaceae), *Cupuliferoi[dae]pollenites* (4.1-10 E; 7.1-10 K; see also Fagaceae), *C.* cf. *parvulus* (7.1-10 K), *C.* sp. (7.1-10 K), *Curvimonocolpites inornatus* (7.1-85 Pa–E), *Diporites* (7.1-49 O, 59 E, 64 E–O), *D. aspis* (7.1-52 O; see also Onagraceae), *Doroteoxylon vicente-peresii* (7.1-54 K), *Dryadopollis minima* (7.1-52 O), *Duplotriporites ariani* (7.1-85 Pa–E), *Echimonocolpites* (7.1-85 Pa–E; 7.2-50 M), *E. densus* (7.1-86 E), *E. ruedae* (7.1-84 Pa), *Echimorphomonocolpites gracilis* (7.1-86 E), *E. soliarius* (7.1-86 E), *Echiperiporites* (4.1-11 O/O–M), *E. akanthos* (7.1-94 O–M,100 K; 7.2-50 M; see also Malvaceae), *E. estelae* (7.1-100 K; 7.2-50 M; see also Malvaceae), *Echistephanocolpites echinatus* (7.1-96 Pa), *Echistephanoporites alfonsi* (7.1-33 Pa, 94 E, 95 Pa), *Echitetracolpites* (?) *tenuiexinatus* (7.1-85 Pa–E), *Echitricolpites* (5.1-7 E; 7.1-85 Pa–E), *E. communis* (7.1-100 K), *E. polaris* (7.1-100 K), *Echitricolporites maristellae* (7.2-50 M), *Echitriporites guianensis* (7.1-94–96 Pa), *E. triangulíformis* (7.1-85 Pa–E, 86 E, 91 E, 100 K; 7.2-43 M; see also Proteaceae), *E. variabilis* (7.1-85 Pa–E), *Elaterocolpites castelaini* (7.1-100 K), *Elateroplicites africaensis* (7.1-100 K), *Elateropollenites jardinei* (7.1-100 K), *Elaterosporites castelaini* (7.1-100 K), *E. klaszi* (7.1-100 K), *E. protensus* (7.1-100 K), *E. verrucatus* (7.1-100 K), *Endressiana brasiliana* (7.1-97a K), *Ephedripites* (7.1-31, 32 Pa), *E. vanegensis* (7.1-96 Pa; see also Other Gymnosperms, Araceae), *Ericipites* (7.1-44 E, 49, 52 O; see also Empetraceae, Ericaceae), *Extratriporopollenites* (4.1-10 E), *E. firmi(u)s* (4.1-8 K), *E.* cf. *longianulus* (4.1-8 K), *Favitricolporites australis* (7.1-29 Pa), *Fenestrites gemmatus* (7.1-100 K), *Foveodiporites guianensis* (7.1-85 Pa–E), *Foveomorphomonocolpites* (*Proxapertites*) *humbertoides* (7.1-80, 82 K; see also Annonaceae), *Foveostephanocolpites perfectus* (7.1-94–96 Pa), *F. typicus* (7.1-95, 96 Pa), *Foveostephanocolporites liracostatus* (7.1-95 Pa), *Foveotricolpites* (7.1-74 K), *F. genuinus* (7.1-86 E), *F. perforatus* (7.1-84, 85 Pa–E, 100 K), *F. pomarius* (7.1-84 Pa), *F. santanderianus* (7.1-84 Pa), *Foveotricolporites caldensis* (7.1-86 E), *F. fossulatus* (7.1-85 Pa–E), *F. marginatus* (7.1-86 E), *F. rugulatus* (7.1-85 Pa–E), *F. voluminosus* (7.1-86 E), *Foveotriporites hammenii* (7.1-85 Pa–E, 86 E), *Fraxinopollenites* cf. *scoticus* (5.1-7 E), *Galeacornea causea* (7.1-100 K), *Gemmamonocolpites amicus* (7.1-86 E), *G. barbatus* (7.1-86 E), *G. gemmatus* (7.1-84 Pa, 85 Pa–E), *G. ovatus* (7.1-86 E), *G. perfectus* (7.1-85 Pa–E), *Gemmastephanocolpites asteroformis* (7.1-94, 95 Pa), *G. gemmatus* (7.1-84 Pa), *Gemmastephanoporites breviculus* (7.1-86 E), *G. polymorphus* (7.1-86 E), *Gemmatricolpites pulcher* (7.1-86 E), *G. subsphaericus* (7.1-29 Pa; see also Aquifoliaceae), *G. vigdisae* (7.1-95, 96 Pa), *Gemmatricolporites berbicensis* (7.1-95, 96 Pa), *G. divaricatus* (7.1-94, 95 Pa), *Glenopollis ornatus* (7.1-52 O; 7.2-8 M), *Gomortegoxylon patagonicum* (7.1-54 K), *Gonzalezoxylon mochaense* (7.1-54 K), *Grimsdalea magnaclavata* (7.2-43, 50 M), *Haloragacidites harrisii* (7.1-29 Pa, 59 E, 64 E–O), *H. trioratus* (7.1-52 O), *Heterocolpites paleocenicus* (7.1-96 Pa; see also Melastomataceae), *H. rotundus* (7.2-50 O), *Hexaporotricolpites emelianovi* (7.1-100 K), *H. lamellaferus* (7.1-100 K), *H. potoniei* (7.1-100 K), *Horniella* (7.1-85 Pa–E), *Intratriporopollenites* (7.1-44 E, 52 O), *Jandufouria minor* (7.1-85 Pa–E), *Janmulleripollis pentaradiatus* (7.1-92 E), *Kachaikena compuesta* (7.1-text reference, K), *Ladakhipollenites rubinii* (7.1-85 Pa–E), *L. simplex* (7.1-85 Pa–E), *Laurinoxylon uniseriatum* (7.2-15), *Laurophyllum chalianum* (7.1-8 K), *L. hickenii* (7.1-8 K), *L. kurtzi* (7.1-8, 14 K), *L. proteaefolium* (7.1-8, 14 K), *Liliacidites* (5.1-7 E; 7.1-10, 20 K, 49, 52 O, 74, 99 K; see also Liliaceae), *L. complexus* (4.1-10 E), *L. crassibaculatus* (7.1-16 K), *L. intermedius* (5.1-5 E), *L. regularis* (7.1-29, 30 Pa), *L. variegatus* (4.1-10 E; 7.1-16, 19 K, 29 Pa, 55 K; see also Palmae), *L. vercireticulatus* (7.1-30 Pa), *Lilicipites variegatus* (7.1-37 Pa; see previous, Palmae), *Longapertites andreisii* (7.1-29 Pa), *L. circulatus* (7.1-86 E), *L. fossuloides* (7.1-86 E), *L. patagonicus* (7.1-29 Pa), *L. proxapertitoides* (7.1-81 K, 84, 85 Pa–E, 86 E, 100 K), *Longitrichotomocolpites triangularis* (7.1-86 E), *Lymingtonia* (?) (7.1-85 Pa–E; see also Nyctaginaceae), *L.* cf. *rhetor* (5.1-7 E), *Magnaperiporites spinosus* (7.1-86 E, 100 K; 7.2-43, 50 M), *Magnatriporites abstractus* (7.1-86 E), *M. umirensis* (7.1-80 K), *Magnotetradites magnus* (7.1-84 Pa), *Malvacipollis tschudyi* (5.1-7 E), *Malvacipolloides comodoroensis* (7.1-52 O; see also Malvaceae), *Maravenites polyoratus* (7.2-43 M), *Margocolporites tenuireticulatus* (7.1-49, 51, 52 O; see also Bignoniaceae), *M. vanwijhei* (7.1-52 O, 100 K; see also Leguminosae), *Menispermites obtusiloba* (7.1-8 K), *M. piatnitzkyi* (7.1-8, 14 K), *Milfordia argentina* (7.1-52 O; 7.2-8 M), *M. minima* (7.1-66 E, O), *Momipites* (7.2-43 M), *M. africanus* (7.1-85 Pa–E, 100 K), *Monocolpites* (7.1-61 E, 66 E–O, 100 K), *M. ruedae* (7.1-81 K), *Monocolpopollenites* (4.1-10 E; 7.1-99 K), *M. ovatus* (7.1-85 Pa–E), *M. spheroides* (7.1-100 K), *M.* aff. *M. tranquillus* (5.1-5 E), *Monocolporites* (4.1-10 E), *Monocotylophyllum heterophyllum* (7.1-74 K), *Monosulcites* (7.1-59 E), *Multiareolites formosus* (7.1-100 K), *Multiporopollenites* aff. *maculosus* (7.1-100 K), *M. pauciporatus* (7.1-85 Pa–E), *Multisiapollis viteauensis* (7.1-49 O; see also Compositae), *Myrtaceidites* (7.1-59, 61 E, 63, 64 E–O; see also Myrtaceae), *M. eugenioides* (7.1-56 Pa), *M.* cf. *mesonesus* (7.1-16 K), *M.* cf. *parvus* (5.1-7 E), *M. verrucosus* (7.1-44, 46 E, 49 O), *Nudopollis terminalis*

(4.1-8 K, 10 E), *N. thiergarti* (4.1-8 K), *Nyssapollenites* cf. *squamosus* (7.1-10 K), *Oculopollis baculotrudens* (4.1-8 K), *Paleosantalaceaepites distinctus* (7.1-85 Pa–E), *Palmoxylon* (4.1-41 Tertiary undifferentiated; see also Palmae), *Papillamonocolpites splendens* (7.1-86 E), *Papillopollis partialis* (7.1-86 E), *Paragonzar(l)ezoxylon chilenomesozoicum* (7.1-54 K), *Paranymphaea proteaefolia* (7.1-8, 14 K; see also Nymphaeaceae), *Parsonidites* (7.1-85 Pa–E), *P. conspicuous* (4.1-11 E, O/O–M), *Parvissacites*? (7.1-100 K), *Peltrandipites* (7.1-99 K), *Penetetrapites mollis* (7.1-99 K), *Pentapsis valdiviae* (7.1-100 K), *Perfotricolpites digitatus* (7.1-86 E, 100 K; see also Convolvulaceae), *P. semistriatus* (7.1-86 E), *Pericolporites* (5.1-7 E), *Periporopollenites demarcatus* (7.1-44 E), *Periretipollis spinosus* (7.1-100 K), *Periretisyncolpites giganteus* (7.1-85 Pa–E), *Perisyncolporites pokornyi* (7.1-100 K; see also Malpighiaceae), *Peromonolites peroreticulatus* (7.1-100 K), *Perseophyllum hauthalianum* (7.1-8 K), *Peumus clarki* (7.1-8 K; genus of Monimiaceae fide Ref. 7.1-25–27 Pa), *Phymopollenites pannosus* (7.1-10 K), *P.* sp. (7.1-10 K), *Plicapollis arcii* (7.1-86 E), *P. bellus* (7.1-80 K), *P. serta* (4.1-8 K), *Poloretitricolpites absolutus* (7.1-85 Pa–E), *Polotricolporites concretus* (7.1-86 E), *P. mocinnii* (7.1-86 E), *P. versabilis* (7.1-86 E), *Poluspissusites* (7.1-49 O; see also Goodeniaceae), *P. puntensis* (7.1-52 O), *Polyadopollenites* (7.1-52 O; see also Leguminosae), *Polyorificites* (7.2-10 M), *Polyplicadites vanegensis* (7.1-94 Pa), *Polyporina* (7.1-59 E), *P. romeroi* (7.1-29 Pa, 50 O), *Populites lancastriensis* (7.1-8 K), *Porocolpollenites* (5.1-7 E; 7.1-11 K), *Proteacidites* (7.1-29 Pa, 46, 59, 61 E, 64 E–O; see also Proteaceae), *P. amolosexinus* (7.1-56 Pa), *P. dehaani* (7.1-65 K–Pa, 80, 100 K), *P. longispinosus* (7.1-100 K), *P. parvus* (7.1-56 Pa), *P. pseudomoides* (7.1-49, 52 O), *P. subscabratus* (7.1-19 K–Pa), *P.* cf. *triangularis* (7.2-50 M), *Proxapertites* (4.1-10 E), *P. cursus* (7.1-85 Pa–E, 96 Pa, 100 K), *P. facetus* (7.1-100 K), *P. magnus* (7.1-85 Pa–E), *P. operculatus* (7.1-94, 96 Pa–E; see also Palmae), *P. psilatus* (7.1-85 Pa–E), *Pseudoplicapollis longiannulata* (4.1-8 K), *Pseudostephanocolpites perfectus* (7.1-86 E), *P.* (?) *verdi* (7.1-86 E), *Pseudovacuopollis* (4.1-8 K), *Pseudowinterapollis couperi* (7.1-46 E, 49 O; see also Winteraceae), *Psilabrevitricolpites* (7.1-85 Pa–E) *Psilabrevitricolporites simpliformis* (7.1-85 Pa–E), *P. triangularis* (7.1-85 Pa–E), *Psiladiporites guianensis* (7.1-94 E), *P. minimus* (7.1-94 O–M), *P. redundantis* (7.1-86 E), *Psilamonocolpites* (7.1-59 E, 64 E–O), *P. grandis* (7.1-85 Pa–E), *P. inornatus* (7.1-94 K, Pa), *P. medius* (7.1-80 K, 94 K, Pa, 96 Pa; see also Palmae), *P. nanus* (7.2-50 M), *Psilaperiporites boliviensis* (7.1-65 K–Pa), *P. minimus* (7.1-66 E–O), *P. multiporus* (7.2-50 M), *P. robustus* (7.1-66 E–O, 100 K), *P. suarezi* (7.1-65 K–Pa), Psila/scabraticolpates (7.1-78d K), *Psilastephanocolpites* (7.1-85 Pa–E), *P. adinos* (7.1-86 E), *P. fissilis* (7.1-94 E), *P. maia* (7.1-95, 96 Pa), *P. marginatus* (7.1-86 E), *P. verrucosus* (7.1-86 E), *Psilastephanocolporites* (7.1-80 K), *P. brevicolpatus* (7.1-85 Pa–E), *P. fissilis* (7.1-56, 95 Pa, 100 K; see also Polygalaceae), *P. matapiorum* (7.2-50 M), *P. schneideri* (7.2-50 M), *Psilastephanoporites* (7.1-85 Pa–E), *P. brasiliensis* (7.1-100 K), *P. stellatus* (7.1-100 K; 7.2-43 M), *Psilasyncolporites* (7.1-85 Pa–E), *P. parvus* (7.1-86 E), *Psilatetradites umirensis* (7.1-94 K), *Psilatricolpites* (7.1-20 K, 66 E–O-80, 99 K), *P. acerbus* (7.1-37 Pa, 86 E; 7.2-50 M), *P. anconia* (7.2-50 M), *P. brevis* (7.1-86 E), *P. ciliatus* (7.1-96 Pa–E), *P. clarissimus* (7.1-94 K), *P. divisus* (7.1-65 K–Pa), *P. fissilis* (7.1-56 Pa), *P. hirsutus* (7.1-96 Pa–E), *P. inargutus* (7.1-29 Pa), *P. minutus* (7.1-56 Pa, 86 E, 96 Pa–E; 7.2-50 M), *P. palaeocenica* (7.1-84 Pa), *P. papilioniformis* (7.1-100 K; 7.2-50 M), *P. patagonicus* (7.1-16 K, 19 K–Pa), *P. polaroides* (7.1-86 E), *P. psilascabratus* (7.1-29 Pa, 50 O), *P. pulcher* (7.2-50 M), *P. pulcherrimum* (7.1-16 K), *P. rubini* (7.1-94 K), *P. simplex* (7.1-37 Pa, 86 E; 7.2-50 M), *P. solus* (7.1-94 E, K, 95, 96 Pa), *P. undamarginis* (7.1-95 Pa), *Psilatricolporites* (7.1-20 K, 29 Pa, 50 O, 56 Pa, 59 E), *P. amagensis* (7.1-87 E), *P. atalayensis* (7.2-50 M), *P. caribbiensis* (7.2-43 M), *P. cereus* (7.1-96 Pa, E), *P. costatus* (7.2-50 M), *P. crassus* (7.1-94 O–M, 96 Pa, E, 100 K, cf. *Pelliceria*), *P. cyanus* (7.2-50 M), *P. divisus* (7.2-43 O–Q), *P. exiguus* (7.2-50 M), *P. florschutzi* (7.1-94 K), *P. garzonii* (7.2-50 M), *P. maculosus* (7.1-66 E–O, 100 K), *P. magniporatus* (7.2-50 M), *P. molinae* (7.1-87 E), *P. normalis* (7.1-86 E), *P. obesus* (7.2-50 M), *P. obscurus* (7.1-86 E), *P. operculatus* (7.1-86 E, 100 K; see also Euphorbiaceae), *P. pachydermatus* (7.2-43 M), *P. patagonicus* (7.1-19 K), *P. rotundiporus* (7.1-94 O–M, 96 Pa, E), *P.* cf. *salamanquensis* (7.1-19 K, 30 Pa), *P. sylvaticus* (7.2-50 M), *P. triangularis* (7.1-94 O–M, 96 Pa, E, 100 K; 7.2-43, 50 M), *P. vanus* (7.1-86 E), *P. varius* (7.2-50 M), *P. venezuelanus* (7.2-43, 50 M), *Psilatriporites sarmientoi* (7.2-50 M), *Psilodiporites redundantis* (5.1-7 E), *Quintinaipollis striatulosa* (7.1-52 O; 7.2-8 M), *Racemonocolpites facilis* (7.1-86 E; see also Palmae), *R. racematus* (7.1-85 Pa–E, 86 E), *R. romanus* (7.1-86 E), *Retibrevitricolpites* (5.1-7 E), *R. catatumbus* (7.1-86 E; 7.2-43, 50 M), *R. increatus* (7.1-86 E), *R. retibolus* (7.1-85 Pa–E, 95 Pa), *R. triangulatus* (7.1-85 Pa–E, 86 E, 91 E, 100 K; 7.2-43 M), *R. yavarensis* (7.2-50 M), *Retibrevitricolporites grandis* (7.1-85 Pa), *R. speciosus* (7.1-85 Pa–E), Reticolpates (7.1-78d K), *Retitricolpites georgensis* (5.1-3 K), *R. sphaeroides* (5.1-3 K), *R. vulgaris* (5.1-2 K), *R.* sp. (5.1-2 K), *Reticulataepollis* cf. *intergranulata* (5.1-7 E), *Reticulatasporites jardinus* (7.1-99, 100 K), *Retidiporites agilis* (7.1-86 E), *R. botulus* (7.1-94–96 Pa, E), *R. elongatus* (7.1-85 Pa–E), *R. magdalenensis* (7.1-80 K, 84 Pa, 94, 96 Pa; see also Proteaceae), *R. poricostatus* (7.1-85 Pa–E), *Retiheterocolpites tertiarius* (7.1-86 E), *Retimonocolpites absyae* (7.2-50 M), *R. bernardii* (7.1-86 E), *R. dividuus* (7.1-74 K), *R.* aff. *Clavatipollenites minutus* (7.1-74 K), *R. longicolpatus* (7.2-50 M), *R. maximus* (7.2-50 M), *R. peroreticulatus* (7.1-99 K), *R. proxaperturoides* (7.1-94 Pa), *R. splendidus* (7.1-86 E), *R. tertiarius* (7.1-86 E), *R.* types 1–5 (5.1-7 E; 7.1-65 K–Pa, 78d K), *Retimonoporites tequendamae* (7.1-94 K), *Retipollenites* (7.1-85 Pa–E), *R.* cf. *confusus* (5.1-7 K), *Retistephanocolpites angeli* (7.1-85 Pa–E, 94–96 Pa; see also Bombacaceae), *R. finalis* (7.1-86 E), *R. fossulatus* (7.1-85 Pa–E), *R. guaduensis* (7.1-94 Pa), *R. minutus* (7.1-86 E), *Retistephanocolporites festivus* (7.1-85 Pa–E, 86 E), *R. fossulatus* (7.1-85), *R. quadriporus* (7.1-94 O–M), *Retistephanoporites angelicus* (7.1-85 Pa–E, 86, 87 E; 7.2-50 M), *R. crassiexinatus* (7.1-85 Pa–E), *R. minutiporus* (7.1-85 Pa–E), *Retisyncolporites angularis* (7.1-85 Pa–E, 86 E), *R. aureus* (7.1-80 K, 86 E), *Retitrescolpites baculatus* (7.1-85 Pa–E), *R. magnus* (7.1-85 Pa–E), *R. peculiaris* (7.1-85 Pa–E), *R. saturum* (7.1-85 Pa–E), *Retitricolpites* (7.1-80 K), *R. absolutus* (7.1-86 E), *R. adeptus* (7.1-86 E), *R. adultus* (7.1-86 E), *R. agricaulis* (7.1-95 Pa), *R. amapaensis* (7.1-100 K; 7.2-43, 50 M), *R. americana* (7.1-66 E–O, 100 K), *R. analemae* (7.1-94 Pa), *R. antonii* (7.1-86 E; 7.2-50 M), *R. bonus*

(7.1-86 E), *R. caquetanus* (7.2-50 M), *R. cecryphalium* (7.1-94–96 Pa), *R. circumcanaliculatus* (7.1-96 Pa), *R. clarensis* (7.1-86 E), *R. colpiconstrictus* (7.2-50 M), *R. conciliatus* (7.1-86 E), *R. constrictus* (7.1-86 E), *R. depressus* (7.2-50 M), *R. florentinus* (7.1-86 E), *R. incisus* (7.1-86 E), *R. herrerae* (7.1-84 Pa), *R. kwakwaniensis* (7.1-94, 95 Pa), *R. lalongatus* (7.1-96 Pa; 7.2-50 M), *R. letitiae* (7.1-94 K), *R. lewisii* (7.2-50 M), *R. magnus* (7.1-86, 91 E), *R. maledictus* (7.1-86, 87 E; 7.2-50 M), *R. maturus* (7.1-86 E; 7.2-50 M), *R. microreticulatus* (7.1-56, 84 Pa, 94 K), *R. minutus* (7.1-86 E), *R. perditus* (7.1-86 E), *R. perforatus* (7.1-86 E), *R. retiaphelis* (7.1-65 K–Pa, 95, 96 Pa, E), *R. reticulatus* (7.1-94 K), *R. saturum* (7.1-86 E), *R. simplex* (7.1-86 E; 7.2-43, 50 M), *R. tuberosus* (7.2-50 M), *R. vulgaris* (7.1-74, 90 K), *R. wijningae* (7.2-50 M), *R.* types 1–6 (5.1-7 E), *Retitricolporites* (7.1-55 K, 59 E, 64 E–O, 80 K), *R. amazonensis* (7.1-66 E–O, 100 K; 7.2-43 M), *R. annaeoides* (7.1-84, 94 Pa), *R. belmontensis* (7.1-100 K), *R.* cf. *brevis* (7.2-43 M), *R. caputoi* (7.2-50 M), *R. chubutensis* (7.1-29, 30, 37 Pa; see also Anacardiaceae), *R. cienaguensis* (7.1-52 O), *R. costatus* (7.1-95, 96 Pa), *R. craceus* (7.1-86 E), *R. crassopolaris* (7.2-50 M), *R. elegans* (7.1-96 Pa, E), *R. ellipticus* (7.2-50 M), *R. equatorialis* (7.1-86 E), *R. finitus* (7.1-86 E), *R. florschutzi* (7.1-94 K, Pa), *R. guianensis* (7.1-94 O–M, 96 Pa, E, 100 K; 7.2-50 M), *R. hispidus* (7.1-86 E, 94 E, O–M, 96 Pa, E; 7.2-43, 50 M), *R. irregularis* (7.1-86, 87 E, 94 O–M, 100 K; see also Euphorbiaceae), *R. latus* (7.2-50 M), *R. leticianus* (7.2-50 M), *R. magnus* (7.1-96 Pa, E), *R. marianis* (7.1-86 E), *R. mariposus* (7.1-94 E, 95, 96 Pa), *R. medius* (7.1-33 Pa, 86, 87 E; 7.2-50 M), *R. microreticulatus* (7.1-65 K–Pa), *R. milnei* (7.2-50 M), *R. oblatus* (7.2-50 M), *R. perpusillus* (7.1-100 K), *R. profundus* (7.1-86 E), *R. pygmaeus* (7.2-50 M), *R. quadrosi* (7.1-100 K), *R. reticulatus* (7.1-94 K), *R. santaisabelensis* (7.2-50 M), *R. saskiae* (7.1-86 E), *R. solimoensis* (7.2-50 M), *R. squarrosus* (7.1-94 O–M, 100 K), *R. ticuneorum* (7.2-50 M), *R. wijmstrae* (7.2-50 M), *Retitriporites amplireticulatus* (7.1-85 Pa–E), *R. dubiosus* (7.1-86 E; 7.2-50 M), *R. federicii* (7.1-86 E), *R. mirabilis* (7.1-100 K), *R. poricostatus* (7.1-85 Pa–E), *R. retibolus* (7.1-94 Pa), *R. tilburgii* (7.1-86 E), *R. typicus* (7.1-86 E), *Reyea polymorphus* (7.1-100 K), *Rhoipites* (7.1-16, 20 K, 46 E), *R. baculatus* (7.1-19 K, 49, 51, 52 O; 7.2-10 M; see also Cunoniaceae, Mimosaceae, Rutaceae), *R. cienagensis* (7.1-85 Pa; 7.2-8, 10 M), *R. cienaguensis* (7.1-49, 52 O; 7.2-13 M), *R. hispidus* (7.1-85 Pa–E), *R. minusculus* (7.1-19 K, 33 Pa; see also Anacardiaceae, Loganiaceae), *R. romeroi* (7.1-52 O), *R. squarrosus* (7.1-85 Pa–E), *Rhoophyllum serratum* (7.1-15 O), *Rogersia australis* (7.1-text reference, K), *Rosannia manika* (7.1-19 K), *Rousea florentina* (7.1-85 Pa–E), *R. georgensis* (7.1-10 K), *R. microreticulata* (7.1-30 Pa), *R. minuscula* (7.1-30 Pa), *R. patagonica* (7.1-29, 33, 37 Pa), *Rouseisporites* (7.1-11 K), *Rubipollis oblatus* (7.1-52 O), *Rugutricolporites felix* (7.1-56, 85 Pa–E, 86 E), *Sapotaceoidaepollenites* (4.1-10 E), *Scabraperiporites nativensis* (7.1-66 E–O, 100 K), *Scabrastephanocolpites* (7.1-85 Pa–E), *S. lisamae* (7.1-84 Pa), *S. scabratus* (7.1-84 Pa), *S. vanegensis* (7.1-84 Pa), *Scabratricolpites simpliformis* (7.1-96 Pa, E), *S. tibialis* (7.1-86 E), *Scabratricolporites planetensis* (7.2-43 M), *Scabratriporites moderatus* (7.1-86 E), *S. redundans* (7.1-86 E; 7.2-50 M), *S. suescae* (7.1-94 Pa), *Schizosporis paleocenicus* (7.1-56 Pa), *S. rugulatus* (7.1-10 K, 56 Pa), *Scollardia trapaformis* (7.1-100 K), *Semitectotriporites gratus* (7.1-86 E), *Siltaria mariposa* (7.1-85 Pa–E), *S. media* (7.1-85 Pa), *Si[e]nipites* (4.1-8 K), *Sofreipites* (7.1-65 K–Pa), *S. legouxae* (7.1-100 K), *Sparcipollis* (7.1-49, 51 O), *Sparganiaceaepollenites* (7.1-29 Pa; see also Sparganiaceae), *Spinitricolpites* (7.1-51 O), *Spinozonocolpites* (7.1-65 K–Pa), *S. baculatus* (7.1-81, 100 K; see also Palmae), *S. breviechinatus* (7.1-85 Pa–E), *S. echinatus* (7.1-66 E–O, 81, 100 K), *S. grandis* (7.1-85 Pa–E), *S. hialinus* (7.1-30 Pa), *S. pachyexinatus* (7.1-85 Pa–E), *Spirosyncolpites clavatus* (7.1-86 E), *S. spiralis* (7.1-85 Pa–E, 86, 87 E; 7.2-50 M), *Stellatopollis* (7.1-74 K), *S. araripensis* (7.1-99 K), *Stephanocolpites evansii* (7.2-43, 50 M), *Stephanocolporites ambigens* (7.1-94 Pa), *Striacolporites pimulus* (7.1-96 Pa, E), *S. tenuissimus* (7.2-43 M), *Striasyncolpites laxus* (7.1-49, 52 O), *S. gamerroi* (7.1-49, 52 O), *Striatopollis exiguus* (7.1-30 Pa), *S. minor* (7.1-85 Pa–E), *S. tenuistriatus* (7.1-85 Pa–E), *Striatricolpites* (7.1-65 K–Pa, 80 K), *S. catatumbus* (7.1-100 K; see also Leguminosae), *S. minor* (7.1-96 Pa, E), *S. saramacensis* (7.1-96 Pa, E), *S. semistriatus* (7.1-86 E), *Striatricolporites digitatus* (7.1-85 Pa–E), *S. gamerroi* (7.1-19 K, 29 Pa, 45 E, 49, 52 O; see also Anacardiaceae), *S. pimulis* (7.1-95, 96 Pa), *Striopollenites dubius* (7.1-100 K), *S. terasmaei* (7.1-100 K), *Symplocoipollenites* (4.1-10 E), *Syncolporites* (7.1-55 K), *S.* cf. *incomptus* (7.2-50 M), *S. lisamae* (7.1-84, 94, 95 Pa; see also Myrtaceae), *S. marginatus* (7.1-85 Pa–E), *S. poricostatus* (7.1-65 K–Pa), *S. triangularis* (7.1-100 K), *Tetracolpites* (7.1-74 K), *Tetracolporites psilatus* (7.1-85 Pa–E), *Tetracolporopollenites spongiosus* (7.1-85 Pa–E), *T. transversalis* (7.1-85 Pa–E), *Tetradites* (7.1-65 K–Pa, 100 K), *T. umirensis* (7.1-81 K), *Thorphyllum patagonia* (7.1-text reference, K), *Tiliapollenites danei* (4.1-11 E), *Tiliaepollenites vescipites* (4.1-10 E; see also Sterculiaceae, Tiliaceae), *Triangulopsis* (7.1-99 K), *Triatriopollenites bertelsii* (7.1-19 K; see also Myricaceae), *T. excelsus* (4.1-8 K), *T. guianensis* (7.1-96 Pa, E), *T. infernalis* (7.1-96 Pa, E), *T. lateflexus* (7.1-19 K; see also Myricaceae, Proteaceae), *T. maedae* (7.1-55 K), *Tricesticillus americanus* (7.1-11 K), *Tricolpites* (7.1-11 K, 59, 61 E, 64 E–O, 74 K), *T. anguloluminosus* (7.1-44 M), *T. antonii* (7.1-85 Pa–E), *T. bibaculatus* (7.1-30 Pa; see also Flacourtiaceae), *T. clarensis* (7.1-85 Pa–E), *T. communis* (7.1-29, 37 Pa), *T. gigantoreticulatus* (7.1-100 K), *T. gillii* (7.1-29 Pa; see also Proteaceae), *T. incisus* (7.1-44 E), *T.* (*Psilatricolpites*) *lumbrerensis* (7.1-34, 35 Pa), *T. microreticulatus* (7.1-55 K), *T. minutus* (7.1-10 K), *T. protoclarensis* (7.1-85 Pa–E), *T. reticulatus[-a]* (7.1-34, 35 Pa, 44, 46 E, 49, 52 O; see also Gunneraceae, Haloragaceae), *T. retielegans* (7.1-16 K), *T. synstriatus* (7.1-65 K–Pa, 100 K), *T. tienabaensis* (7.1-100 K), *T. trioblatus* (7.1-49, 52 O; 7.2-8 M), *T.* sp. (7.1-16 K), *T.* cf. *variofoveatus* (4.1-10 E), *Tricolpollenites minutus* (5.1-3 K), *T. polyhedrus* (5.1-3 K), *Tricolporites* (7.1-11, 16 K-59 E, 65 K–Pa), *T. microreticulatus* (7.1-61 E; *T. reticulatus*, *Gunnera*, fide Wanntorp et al. 2004b), *Tricolpopollenites fallax* (7.1-55 K), *Tricolporopollenites distinctus* (7.1-93 K), *T. hians* (7.1-66 E–O), *T. microporifer* (7.1-55 K), *T. minor* (7.1-55 K), *T. punctulosus* (7.1-55 K), *Tricornites elongatus* (7.1-65 K–Pa, 100 K), *Trichotomocolpites* (7.2-43 M), *Trifossapollenites* (7.1-100 K), *Trifurcata flabellata* (7.1-97a K), *Triorites* (7.1-33 Pa, 65 K–Pa), *T. edwardsii* (7.1-56 Pa), *T. harrisii* (7.1-56 Pa), *T. minor* (7.1-16 K, 46 E, 52 O, 56 Pa), *T. minusculus* (7.1-16 K), *T. minutipori* (7.1-56 Pa), *Triporites* (7.1-80 K), *T. africaensis* (7.1-100 K), *T. iversenii* (7.1-81 K), *T. suescae*

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"[Any] book without an index should be damned ten miles beyond hell…" (Attributed to John Baynes via Francis Douce by William Thoms, *Notes and Queries*, August 4, 1877; also attributed to Thomas Carlyle in Boorstin, 1983, p. 532.)

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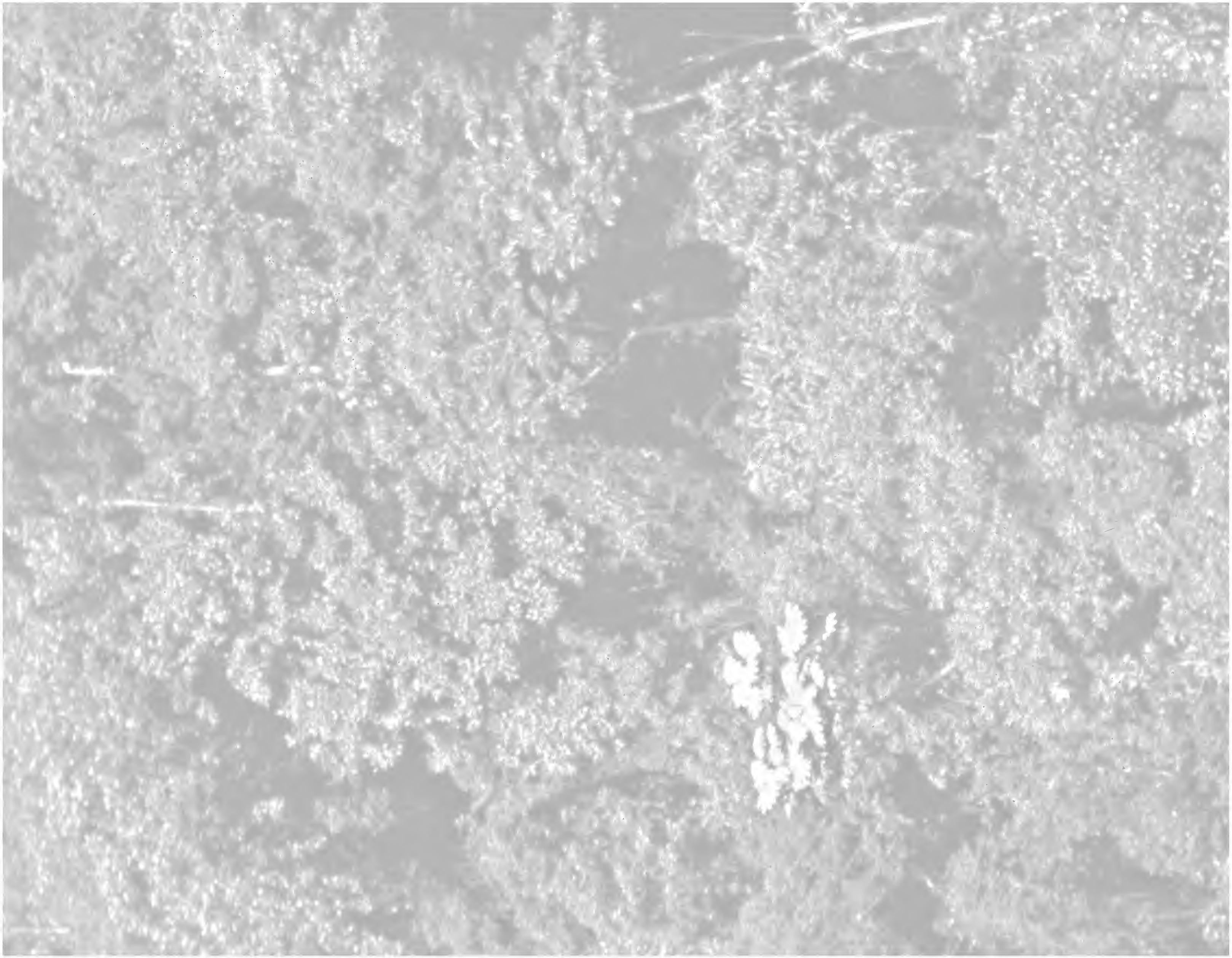
(Mesozoic and Cenozoic Eras)

	Quaternary Period	
	Holocene Epoch	11,500
	Pleistocene	2.6 MA
	Tertiary	
	Pliocene	
	Piacenzian Stage	3.6
	Zanclean	5.3
	Miocene	
	Messinian	7.2
	Tortonian	11.6
	Serravallian	13.6
Cenozoic Era	**Langhian**	15.9
	Burdigalian	20.4
	Aquitanian	23.0
	Oligocene	
	Chattian	28.4
	Rupelian	33.9
	Eocene	
	Priabonian	37.2
	Bartonian	40.4
	Lutetian	48.6
	Ypresian	55.8
	Paleocene	
	Thanetian	58.7
	Seldanian	61.7
	Danian	65.5
	Cretaceous	
	Senonian	
	Maastrichtian	70.6
	Campanian	83.5
	Santonian	85.8
	Coniacian	89.3
	Gallic	
Mesozoic Era	**Turonian**	93.5
	Cenomanian	99.6
	Albian	112.0
	Aptian	125.0
	Barremian	130.0
	Neocomian	
	Hauterivian	136.4
	Valanginian	140.2
	Berriasian	145.5
	Jurassic	
	Triassic	

Conversion table for United States customary and metric units of measurements

acre	**0.4 hectare**
hectare	**2.7 acres**
feet to meters	**multiply by 0.3048**
meters to feet	**multiply by 3.2808**
miles to kilometers	**multiply by 1.6093**
kilometers to miles	**multiply by 0.6213**
inches to millimeters	**multiply by 25.4**
millimeters to inches	**multiply by 0.0393**
mi^2 to km^2	**multiply by 2.590**
km^2 to mi^2	**multiply by 0.3861**
°F to °C	**5/9 (°F – 32°)**
°C to °F	**9/5 (°C + 32°)**